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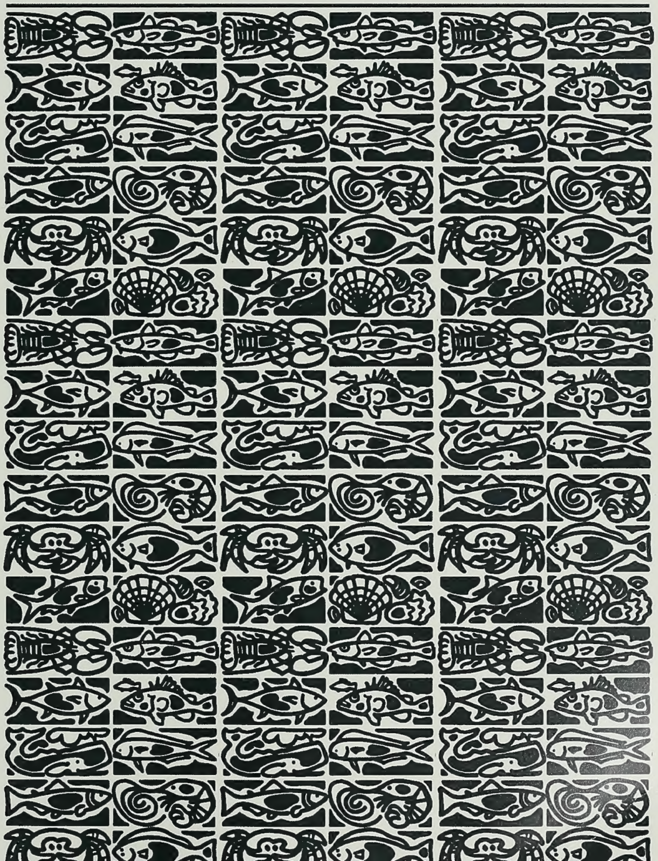

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Spencer F. Baird
First U.S. Commissioner
of Fisheries and founder
of *Fishery Bulletin*

Functional foraging habits and dietary overlap of yellowfin sole (*Limanda aspera*) and northern rock sole (*Lepidopsetta polyxystra*) in a coastal nursery of the Bering Sea

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Abstract—Understanding patterns of foraging and competition in nursery habitats can elucidate patterns of productivity in multispecies fisheries. Yellowfin sole (*Limanda aspera*) and northern rock sole (*Lepidopsetta polyxystra*) co-occur throughout the Bering Sea where they support major fisheries. We examined the diets and foraging ecology of juvenile yellowfin sole and northern rock sole (35–100 mm in standard length) captured along the north side of the Alaska Peninsula and in the Port Moller-Herendeen Bay system, the largest marine embayment in the southeastern Bering Sea. As observed in other parts of their ranges, the diets of both species included polychaetes and amphipods. The primary difference in the diets of these species was that the prey of yellowfin sole were almost exclusively endobenthic and epibenthic invertebrates (>82.7% by weight combined) and the northern rock sole consumed substantial amounts of hyperbenthic mysids and pelagic euphausiids (42% combined). Overall dietary overlap was low (Schoener index [SI]=0.39), in part due to differences in microhabitat use. At sampling stations where both species co-occurred, dietary overlap was notably higher (SI=0.55). Patterns of functional foraging habits and juvenile niche separation that facilitate coexistence of these species throughout their range were expressed with a novel application of principal components analysis of the abiotic (habitat characteristics) and biotic (consumer traits) factors associated with commonly occurring prey types.

Understanding how species respond to variation in their environment and how they interact with their prey, predators, and competitors is critical to predicting the consequences of climate change on marine ecosystems and fisheries. Many ecosystems include pairs or groups of ecologically and morphologically similar species that co-occur in space and time. Niche separation or partitioning is generally assumed to be a critical component of community ecology allowing such species to coexist. Conversely, niche overlap is generally assumed to support ecosystem stability through efficient utilization of available resources and buffering of predator–prey linkages (Neutel et al., 2002). In the marine environment, niche partitioning and overlap are most commonly described by using physical habitat associations and diet composition (Ross, 1986).

There is a diverse assemblage of 24 flatfish species in the Gulf of Alaska (GOA) and Bering Sea (Mecklenburg et al., 2002), of which 13 species are commercially harvested (Fissel et al., 2021). In the southeastern Bering Sea (SEBS), harvest is focused on yellowfin sole (*Limanda aspera*) and northern rock sole (*Lepidopsetta polyxystra*), with several other species harvested at lower rates (Fissel et al., 2021). The yellowfin sole supports the largest fishery (by landings) of any flatfish species, worldwide. Although abundances of both species recovered from overharvesting in the 1960s and 1970s, spawning biomass of yellowfin sole has been in general decline since a peak was reached in the mid-1990s (Wilderbuer et al., 2018). Throughout their ranges, these species have overlapping distributions on the continental shelf, indicating the potential for competition.

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Nursery habitats of flatfish species are a finite space in a 2-dimensional environment where density-dependent and density-independent factors can contribute to survival and recruitment variation (Nash and Geffen, 2012). Like juveniles of many other flatfishes, juvenile yellowfin sole and northern rock sole reside in coastal waters and commonly co-occur throughout their range. The value of coastal waters as nursery habitats is frequently enhanced through warm temperatures favorable to growth, high productivity of prey resources (Wouters and Cabral, 2009), and reduced abundances of large predators (Paterson and Whitfield, 2000). Of course, the use of these nursery habitats by multiple species may increase the potential for competition.

Previous work on the feeding habits of shallow-water flatfishes in both the GOA and SEBS has revealed diets commonly dominated by polychaetes, amphipods, and copepods, with bivalves, mysids, and cumaceans being important to some species (Holladay and Norcross, 1995; Lang et al., 1995; Hurst et al., 2007; Yeung and Yang, 2017). The amount of dietary overlap among species and age classes varies considerably. In the SEBS, diets of yellowfin sole and northern rock sole have been examined in deeper areas (depths >30 m) of the shelf but not in nearshore areas along the Alaska Peninsula.

In this study, we examined the foraging habits of juvenile yellowfin sole and northern rock sole in nearshore waters of the SEBS along the Alaska Peninsula and within the Port Moller-Herendeen Bay (PM-HB) system, the largest coastal embayment of the SEBS. We focused on functional aspects of foraging and associations between diet and habitat selection that influence competition between these important species. The data from this work fill a gap and provide a baseline for future examination of the effects of climate on foraging patterns of these important flatfishes in the SEBS.

Materials and methods

Field collections

The SEBS is bordered on the east by the Alaska mainland and on the south by the Alaska Peninsula (Fig. 1). The region is characterized as a broad, gradually sloping shelf of mixed mud and sand sediments (Hurst, 2016). The PM-HB system is the largest inlet on the north side of the Alaska Peninsula. The system is a shallow (depths mostly <10 m), tidally dominated marine inlet, although the head of Herendeen Bay is fjord-like with depths up to 100 m.

Sampling for juvenile flatfish in Port Moller (in both the inner and outer regions, IPM and OPM regions), Herendeen Bay (HB region), and the adjacent coastal waters of the Bering Sea (BC region) was carried out in August 2012 aboard the 13-m chartered FV *Bountiful*. A total of 75 tows were completed by using a beam trawl with a width of 3 m, height of 0.78 m, 7-mm mesh body, and 4-mm-mesh codend (Abookire and Rose, 2005). Depth of tows ranged from 2 to 30 m, and tows were conducted during daylight hours. The net was towed at 1.5 kt (0.77 m/s) for 5 min at each sampling station against the prevailing current. The length of each tow was measured by using a global positioning system. Juvenile flatfish ≤125 mm in standard length (SL) were frozen for laboratory processing. In the field, larger fish were identified to species, and their lengths were measured. The epibenthic macroinvertebrate fauna at each station was described by estimating the catch of crangonid shrimp and weighing all other benthic invertebrates in major functional groups (seastars, hermit crabs, other crabs, anemones, sand dollars, urchins, sponges, gastropods, and bivalve shells). Additional details on sampling, including catch rate at each station, can be found in Hurst (2016).

Bottom water temperature and salinity were measured with a YSI Model 85[1] instrument (YSI Inc., Yellow Springs, OH) at the midpoint of the tow. Surface sediments were collected at this location with a Ponar grab and frozen for laboratory analysis. For analysis, approximately 15 g of sediment was washed through a 62-µm sieve, dried, and sorted with a mechanical shaker. Grain size distribution was reported as the fractions of silt-clay (<6.25 µm), fine sand (62.5–250 µm), medium sand (250–500 µm), coarse sand (0.5–2 mm), and gravel (>2 mm). A separate sample was dried and burned at 550°C for determination of organic content of surface sediments.

Laboratory examination

Fish from the field were thawed and blotted dry, and species identifications were confirmed. Standard length (to the nearest millimeter) and weight (to the nearest 0.01 g) were measured. From fish <100 mm SL, stomachs were excised from the esophagus to the pyloric caeca and preserved in 10% buffered formalin for a minimum of 2 weeks prior to identification of stomach contents. The stomach was opened, and the bolus was extracted, blotted dry, and weighed (to the nearest 0.0001 g). The bolus was examined under a compound microscope, and prey taxa were identified to the lowest possible taxon, with the majority (67%) identified to family level. Items from the stomach were grouped into categories of identifiable taxa, enumerated, blotted dry, and weighed. Stomach fullness of each fish was calculated as a percentage of body mass (excluding the mass of prey items).

All identified prey items were associated with their AphiaID, which can be found in the World Register of Marine Species (WoRMS, available from website, accessed July 2015). The AphiaID is a searchable, unique, and stable identifier that provides taxonomic quality control (Vandepitte et al., 2015). Prey items were grouped into 4 functional habitat categories based on life history characteristics and habitat occupancy during daylight hours. The categories were endobenthic, epibenthic, hyperbenthic, and pelagic. The habitat categorization of prey taxa is used as an indication of the foraging mode, activity level,

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[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

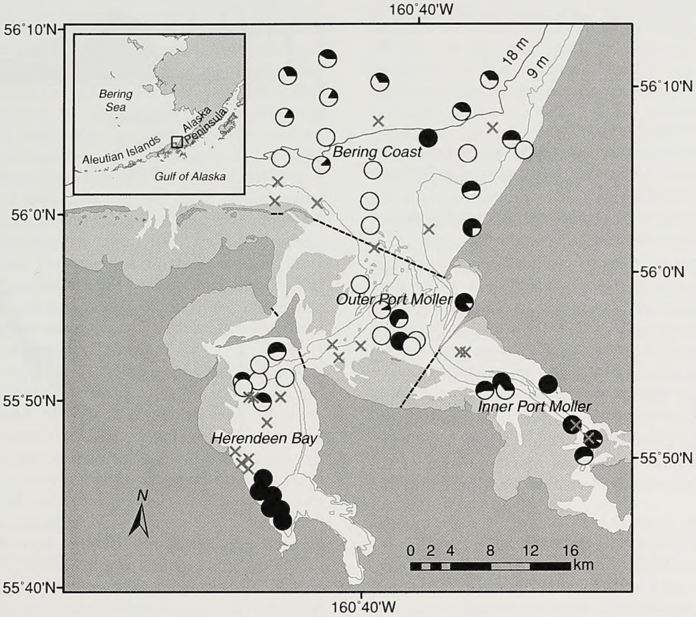

Figure 1

Map of the Port Moller-Herendeen Bay (PM-HB) system, with the inset showing the location of the PM-HB system along the Alaska Peninsula. Pie symbols indicate sampling locations, and the colors in these symbols indicate proportions of catch at each sampling station composed of yellowfin sole (*Limanda aspera*) (black) and northern rock sole (*Lepidopsetta polyxystra*) (white). Gray × symbols indicate stations where neither species was captured. Regions within the sampling area are Bering Sea coastal waters (Bering Coast), Herendeen Bay, the Outer Port Moller, and the Inner Port Moller. Dashed lines indicate borders between regions. Areas in a light gray shade are intertidal habitats. Gray lines indicate depth contours.

and off-bottom activity of juvenile flatfish. The endobenthic category is for organisms, such as polychaetes and bivalves, that live within the sediment. Epibenthic organisms, such as barnacles and most harpacticoids, are directly associated with the sediment surface. Hyperbenthic organisms are those that spend part or all of their time associated with the sediment but are more mobile than epibenthic organisms (Mees and Jones, 1997). Pelagic organisms inhabit the surface or water column and do not come in regular contact with the bottom.

Prey taxa richness and sampling coverage

Total species richness of the prey in diets of yellowfin sole and northern rock sole in the sampling area was estimated from extrapolation of the relationship of species richness and sample size by using the function iNEXT in the package iNEXT (vers. 2.0.20; Chao et al., 2014; Hsieh et al., 2016, 2020) in statistical software R (vers. 4.0.5; R Core Team, 2021), with 95% confidence intervals calculated with 1000 bootstrap iterations. Non-prey (e.g., sand) and unidentifiable items were removed from all analyses. Practical limitations to prey identification resulted in prey types reflecting different levels of taxonomic aggregation. Sampling coverage provided an estimate of diet completeness, where the probability of encountering a new prey taxa in the next independent observation is 1 minus the sampling coverage from the last observed sample (Hsieh et al., 2016).

Diet descriptions

To correct diet compositions for uneven sampling coverage (stations with high catch rates represented by proportionally fewer diet samples), prey mass was weighted on the basis of the catch rates at each station by using this equation:

$$W'_{\mathrm{i}} = \frac{W_{\mathrm{i}} \times CPUE_{\mathrm{s,a,q}}}{n_{\mathrm{s,a,q}}}, \tag{1}$$

where W_{i} = the mass of prey taxon i;

$CPUE_{\mathrm{s,a,q}}$ = the catch per unit of effort for age a of species s at sampling station q (number of individuals per 250 m^2); and

$n_{\mathrm{s,a,q}}$ = the number of stomachs analyzed for age a of species s at station q.

Fish age groups were based on the length–frequency modes provided in Hurst (2016).

The prey-specific index of relative importance (PSIRI) (Brown et al., 2012) was calculated for each identified prey type to distinguish prey species and prey habitat categories that dominated the diets of northern rock sole and yellowfin sole. The PSIRI accounts for biases inherent in the standard index of relative importance of frequently occurring prey (Brown et al., 2012). The PSIRI is additive; therefore, it clarifies representation of the various levels of taxonomic identification inherent in diet studies:

$$PSIRI = \frac{\frac{n_{\mathrm{i}}}{n}\left(\frac{\sum_{\mathrm{j=1}}^{\mathrm{n}} \%N_{\mathrm{ij}}}{n_{\mathrm{i}}} + \frac{\sum_{\mathrm{j=1}}^{\mathrm{n}} \%W_{\mathrm{ij}}}{n_{\mathrm{i}}}\right)}{2}, \tag{2}$$

where $\%N_{\mathrm{ij}}$ = the weighted number of prey category i in stomach j;

$\%W_{\mathrm{ij}}$ = the weighted cumulative mass of prey category i in stomach j;

n = the total number of stomachs with identifiable prey; and

n_{i} = the total number of stomachs containing prey i.

Dietary overlap coefficients were calculated between flatfish species by using samples from all sampling stations and from only those stations where the species co-occurred. Dietary overlap was based on the Schoener Index (SI), which was calculated as follows:

$$SI = 1 - \frac{1}{2}\left(\sum\nolimits_{\mathrm{i}} | p_{\mathrm{ij}} - p_{\mathrm{ik}} |\right), \tag{3}$$

where p_{ij} = the proportion by weight of prey i by group j; and

p_{ik} = the proportion by weight of prey i by group k.

The general patterns of dietary overlap are based on analyses across the full size range (35–99 mm SL) (Fig. 2). We also examined the potential effect of size variation on dietary overlap by using analyses that examined overlap in 2 size classes (small: <66 mm SL; large: ≥66 mm SL) and by restricting data used in analysis to overlapping sizes observed in the study area (44–90 mm SL).

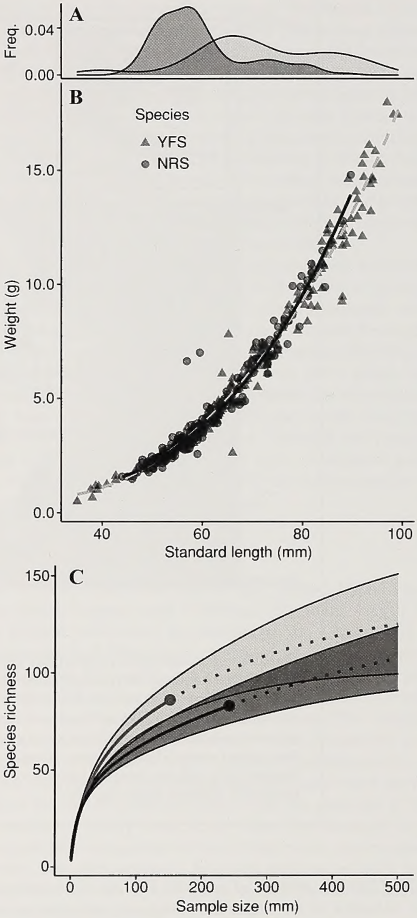

Figure 2

(A) Length–frequency distributions and **(B)** length–weight relationships of yellowfin sole *(Limanda aspera)* (YFS) (light gray area and dashed gray line) and northern rock sole *(Lepidopsetta polyxystra)* (NRS) (dark gray area and solid black line) that were collected in a coastal nursery in the Bering Sea in August 2012 and that had their stomach contents analyzed. **(C)** Estimated species richness for prey in diets of each species based on the relationship of species richness to sample size. In panel C, for YFS (gray) and NRS (black), the circles indicate the total number of samples, the solid lines indicate interpolated estimates, and the dotted lines indicate extrapolated estimates; the light and dark gray bands indicate the 95% confidence intervals.

Foraging patterns

We discerned the functional foraging patterns of yellowfin sole and northern rock sole with a principal components analysis (PCA) of the environmental and biophysical features of the predation conditions for each prey taxa. This approach differs from the nonmetric multidimensional scaling analysis frequently applied in diet studies. Whereas the nonmetric multidimensional scaling approach is an ordination of samples based on the degree of co-occurrence of prey types in the diets of individual predators (or pooled by sampling location), our approach focuses on ordination of the characteristics that describe the predation event. For example, in this approach, prey taxa would be clustered in the ordination space if they were consumed at similar depths, at similar times of day, by similarly sized predators, even if they rarely co-occurred in the diets of individual predators.

For this analysis, prey taxa were grouped into broad taxonomic and habitat categories (e.g., epibenthic copepods) and retained in the analysis if they occurred ≥3 times in the diets of either predator species. The matrix for each prey taxa was created by using the mean of each variable from all observations of that prey taxa. We limited the number of response variables in the prey taxa matrix to reduce occurrences of highly correlated variables. However, because of their traditional importance to habitat definitions, bottom water temperature and depth were retained despite their strong negative correlation (coefficient of determination [r^2]>0.7), and all sediment fractions were retained despite an r^2>0.7 for some combinations. Variables included in the analysis were consumer SL, K (Fulton's condition factor), and stomach fullness; log-transformed catch per unit of effort for the species at the station; and the corresponding environmental variables of time of day, depth, bottom water temperature, sediment proportions of silt or clay, fine sand, medium sand, coarse sand, granules, and bivalve shells. Fractions of sediment composition were logit transformed prior to analyses, and all variables were standardized prior to analyses. A single PCA of the combined prey of northern rock sole and yellowfin sole was conducted.

Results

Collections

Within the PM-HB system, juvenile yellowfin sole were more abundant than northern rock sole, but northern rock sole were more abundant in the coastal waters outside the mouth of the PM-HB system. Both species were found in all sampling areas except for the innermost stations of the HB region where only yellowfin sole were caught (Fig. 1). At least one of the species was captured at 47 of the 75 sampling stations, with both species being captured at 24 stations. Yellowfin sole (35–99 mm SL) and northern rock sole (44–90 mm SL) analyzed for this study were age 1 and age 2 (based on length–frequency distributions). A cohort of smaller age-0 northern rock sole (<35 mm SL) (Hurst, 2016) captured during sampling is not described here.

In total, diets of 443 juvenile flatfish were examined (260 northern rock sole and 183 yellowfin sole). Overall, mean stomach fullness was significantly higher in northern rock sole (1.77% [standard error of the mean (SE) 0.14]) than in yellowfin sole (0.22% [SE 0.02]) (analysis of variance: P<0.001). Although this pattern was consistent across sampling regions, it was most pronounced in the BC region, with mean stomach fullness of northern rock sole at 2.18% (SE 0.19). Although samples were collected only during daylight hours (0800–2100), there was a clear pattern of feeding periodicity for northern rock sole with maximum stomach fullness observed in fish caught during 1600–1800 (Fig. 3). There was no temporal pattern in stomach fullness observed for yellowfin sole.

Diet breadth

We identified 91 distinct prey types in the diets of yellowfin sole and 85 distinct prey types in the diets of northern rock sole. Some of these prey types were common prey items that were identified to life stage within a species; whereas, other types were identifiable only to order or family. Estimates of cumulative prey richness of the diet of yellowfin sole and northern rock sole were 151.1 (SE 30.0) and 129.8 (SE 22.6), respectively, and estimates were not significantly different between predator species

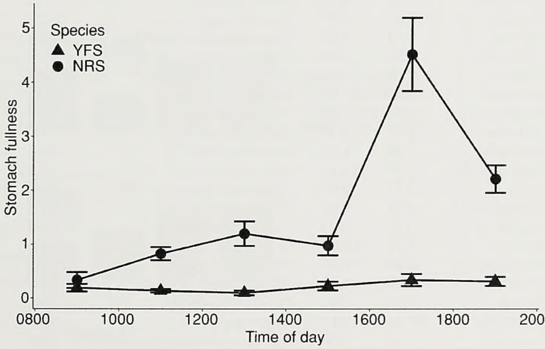

Figure 3

Temporal pattern in stomach fullness of yellowfin sole (*Limanda aspera*) (YFS) and northern rock sole (*Lepidopsetta polyxystra*) (NRS) captured in August 2012 in coastal areas of the southeastern Bering Sea. Error bars indicate standard errors of the mean.

(Fig. 2). Sampling coverage for each predator species was above 90%, indicating a robust description of prey diversity within the diets of yellowfin sole (93.7% [SE 1.9]) and of northern rock sole (97.1% [SE 0.8]) (Fig. 2).

Diet composition

Copepods, polychaetes, amphipods, and mysids were most important in the diets of both flatfish species (on the basis of PSIRI) (Table 1; for complete diet composition with all prey taxa identified from stomach contents, see Supplementary Table [online only]). Copepods were the dominant prey category for both northern rock sole and yellowfin sole, with PSIRI values of 31.4% and 32.6%, respectively. Within the copepod group, an epibenthic harpacticoid, *Ectinosoma* sp., was the most important prey item for both species, with yellowfin sole also consuming significant amounts of hyperbenthic *Eurytemora herdmandi*. Polychaetes were the next most important prey group for both species with PSIRI values of 29.3% for yellowfin sole and 19.1% for northern rock sole. Although most polychaetes could not be identified to family or genus, of those identified, the family Ampharetidae was the greatest contributor to the diets of both species. Amphipods had PSIRI values of 18.6% for yellowfin sole and 15.5% for northern rock sole. Yellowfin sole consumed a diversity of amphipod species, but amphipod consumption by northern rock sole was dominated by *Liljeborgia* spp., *Metaphoxus* spp., and *Photis* spp. Mysids had a PSIRI of 16.0% for northern rock sole but had a PSIRI of only 4.8% for yellowfin sole.

The prey category that differed the most between the diets of the 2 flatfish species was euphausiids, which were rare in the diets of yellowfin sole (PSIRI=0.8%) but common in the diets of northern rock sole (PSIRI=11.1%). *Thysanoessa raschii* accounted for the majority of euphausiids consumed by northern rock sole.

When diet composition was expressed in percentage by weight (%W′) of prey types, the same groups were

Table 1

Prey-specific index of relative importance (PSIRI) of the taxa of primary prey found in stomach contents of yellowfin sole (*Limanda aspera*) (YFS) and northern rock sole (*Lepidopsetta polyxystra*) (NRS) sampled in coastal areas of the southeastern Bering Sea in August 2012. Values for the 4 primary groups, Amphipoda, Copepoda, Mysidae, and Polychaeta, in the diets of sampled fish are presented, with additional details at a higher taxonomic resolution. Values are provided only for prey groups with PSIRI values ≥0.01. For complete diet composition with all prey taxa identified from stomach contents, see Supplementary Table (online only). BL=body length.

Taxonomic groups			Breakdown of taxa in primary groups					
Prey group	YFS	NRS	Prey taxa	YFS	NRS	Prey taxa	YFS	NRS
Amphipoda	18.55	15.52	AMPHIPODA			COPEPODA		
Arthropoda	0.29	0.00	*Atylus collingi*	0.52	0.00	*Ectinosoma* spp.	24.40	30.89
Bivalvia	0.64	0.07	*Caprella* spp.	0.24	0.00	Ectinosomatidae	2.67	0.28
Bryozoa	0.01	0.00	Caprellidae <4 mm BL	0.04	0.01	*Eurytemora herdmandi*	5.33	0.18
Cirripedia	0.58	0.00	Caprellidae >4 mm BL	0.03	0.00	*Oithona* spp.	0.10	0.00
Cnidaria	2.60	0.00	*Dyopedos unispinus*	2.04	0.02	*Stephos* spp.	0.01	0.00
Copepoda	32.62	31.35	*Eohaustorius* spp.	0.02	0.00	*Tigriopus* spp.	0.06	0.00
Crustacea	0.01	0.00	Gammaridea	2.16	6.50	*Tisbe* spp.	0.04	0.00
Cumacea	4.37	2.48	*Gammaropsis* spp.	1.56	0.00	*Zaus* spp.	0.01	0.00
Decapoda	2.88	1.25	Ischyroceridae	0.13	0.04	MYSIDAE		
Euphausiacea	0.76	11.14	*Ischyrocerus* spp.	0.62	0.43	Mysidae, juvenile/adult	0.55	2.17
Pisces	0.71	0.00	*Liljeborgia* spp.	0.82	3.53	Mysidae, larvae	1.07	5.36
Gastropoda	0.27	0.00	Lysianassidae	0.53	0.07	*Neomysis kadiakensis*	2.62	6.24
Isopoda	0.13	0.03	*Metaphoxus* spp.	0.00	1.94	*Pacifiacanthomysis nephrophthalma*	0.01	0.00
Mysida	4.79	15.99	*Orchomene* spp.	0.57	0.12			
Nematoda	0.39	0.23	*Orchomenella* spp.	0.37	0.00	*Xenacanthomysis pseudomacropsis*	0.54	2.22
Ostracoda	0.05	0.00	*Pacifoculodes zernovi*	2.64	1.19			
Plantae	0.76	0.24	*Photis macinerneyi*	1.44	0.63	POLYCHAETA		
Polychaeta	29.34	19.12	*Photis* spp.	3.10	0.00	Ampharetidae	6.25	2.87
Tunicata	0.02	0.00	*Podoceropsis chionocetophilia*	0.82	0.90	Maldanidae	0.64	0.69
Other	0.48	0.08	*Ramellogammarus vancouverensis*	0.62	0.00	Nereididae	1.46	0.21
						Onuphidae	0.65	2.71
			Wecomedon similis	0.15	0.14	Phyllodocidae	1.05	1.30
			Unidentified Amphipoda	0.13	0.00	Spionidae	4.90	1.66
						Terebellidae	0.75	0.01
						Unidentified Polychaeta	13.64	9.67

identified as the primary contributors except that copepods appeared less important than when expressed in PSIRI values (Fig. 4A). Examination of diets by using the functional habitat categories of the prey revealed that yellowfin sole consumed primarily endobenthic prey (%W′=66.0%), predominantly polychaetes with lesser amounts of epibenthic and hyperbenthic prey. The diet of northern rock sole also included a high proportion of endobenthic prey (%W′=42.5%), but they foraged much more extensively on hyperbenthic and pelagic prey (combined %W′=45.8%), primarily mysids and euphausiids.

Polychaetes were the dominant prey in all sampling regions for both flatfishes (%W′=33.3–65.7%), but there were spatial differences in contributions of secondary prey types (Fig. 4). For yellowfin sole, copepods were most important in the HB region (%W′=27.4%), hydrozoans were common in the IPM and OPM regions (%W′~13%), and amphipods (%W′=28.0%) and mysids (%W′=12.9%) were common in samples collected in the BC region. For northern rock sole, copepods were most important in the HB region (%W′=31.9%), and decapods were common in the IPM region (%W′=16.5%). Mysids (%W′=20.9%) and euphausiids (%W′=26.2%) were most commonly consumed in the BC region. Endobenthic prey dominated the diets of both species in the IPM and OPM regions, with other functional categories making significant contributions in other regions. Hyperbenthic and pelagic prey contributed the most to diets of yellowfin sole in the HB region and northern rock sole in the BC region.

Yellowfin sole and northern rock sole had low levels of dietary overlap across the study area, with an overall SI of 0.39. This low overlap was in part a result of spatial segregation because overlap was notably higher (SI=0.55) when calculated by using only fish collected at sampling stations where the species co-occurred. Within sampling regions, dietary overlap was highest in the HB region (SI=0.53) and lowest in the OPM region (SI=0.15).

The low level of dietary overlap does not appear to have been driven by differences in body size of yellowfin sole and northern rock sole captured in the study area. The

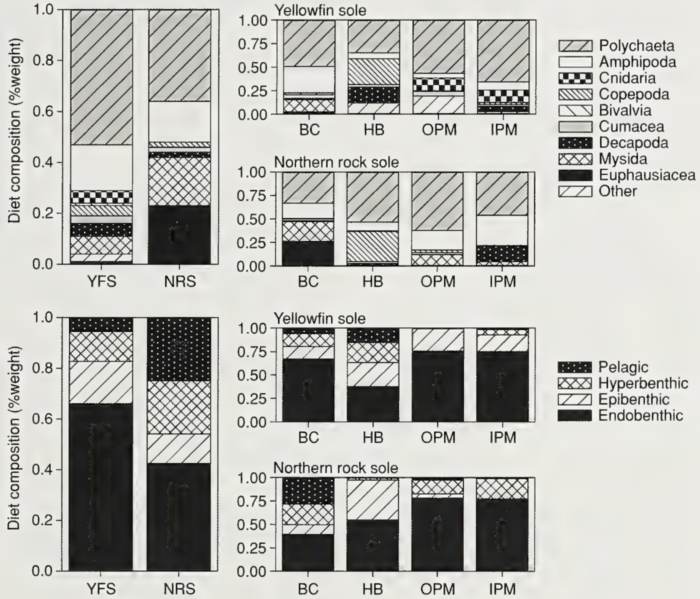

Figure 4

Diet composition in percentages by weight based on taxa identified in stomach contents of yellowfin sole (*Limanda aspera*) (YFS) and northern rock sole (*Lepidopsetta polyxystra*) (NRS) captured in coastal areas of the southeastern Bering Sea in August 2012. The top group of graphs categorizes prey taxonomically, and the bottom group of graphs categorizes prey by functional habitat. Graphs on the right present diets by sampling region in the study area: Bering Sea coastal waters (BC), Herendeen Bay (HB), the Outer Port Moller (OPM), and the Inner Port Moller (IPM).

index values for dietary overlap observed within small (<66 mm SL: SI=0.42) and large (≥66 mm SL: SI=0.34) size classes was similar to that observed across the full size range of sampled fish (SI=0.39). Results of comparisons of overlap across size classes within species indicate more dietary overlap between size classes of northern rock sole (SI=0.70) than those of yellowfin sole (SI=0.40).

Foraging characterization

Results of PCA reveal similarities and differences in foraging patterns between yellowfin sole and northern rock sole. The first principal component (PC1) explains 41.8% of the variance and reflects differences in general foraging habitat between yellowfin sole and northern rock sole (flatfish species was not itself used as a response variable) (Fig. 5). Yellowfin sole consumed prey in areas with higher temperature, shallower depths, and finer sediments than the areas where northern rock sole consumed prey (PC1: |coefficient of correlation [*r*]|>0.72). The PC1 is also strongly correlated with stomach fullness and time of sampling, reflecting the diel pattern of feeding and overall higher levels of stomach fullness for northern rock sole. The second principal component (PC2) explains 22.6% of the variance and is associated with the gradient between fine sand and larger sediments (medium sand, coarse sand, granules, and shells).

The PC1 scores for euphausiids and mysids consumed by both species are notably higher than those for other prey items, reflecting that their consumption occurred in deeper, cooler habitats. Euphausiids had the greatest mean depth and lowest temperature of occurrence in the diets of

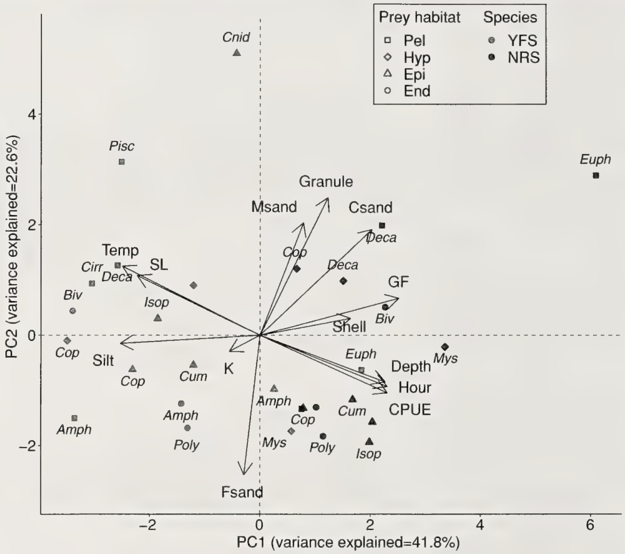

Figure 5

Principal component analysis of foraging patterns of yellowfin sole (*Limanda aspera*) (YFS) and northern rock sole (*Lepidopsetta polyxystra*) (NRS) captured in coastal areas of the southeastern Bering Sea in August 2012. Analysis is based on the mean value of biotic and abiotic conditions averaged across all occurrences of each prey type in stomachs of each predator species. Prey are grouped by taxonomy and habitat associations relative to the benthos: endobenthic (End), epibenthic (Epi), hyperbenthic (Hyp), and pelagic (Pel). Traits of predators are standard length (SL), stomach (gut) fullness (GF), and Fulton's condition factor (K). Traits of sampling stations are depth; temperature (Temp); sediment fractions of silt or clay (Silt), fine sand (Fsand), medium sand (Msand), coarse sand (Csand), granules, and shells; time of sampling (Hour); and catch per unit of effort (CPUE) for the predator species. Prey taxa include Polychaeta (Poly), Amphipoda (Amph), Cnidaria (Cnid), Copepoda (Cop), Bivalvia (Biv), Cumacea (Cum), Decapoda (Deca), Mysida (Mys), Euphausiacea (Euph), and Pisces (Pisc).

both predator species. Conversely, hyperbenthic copepods (low PC1 scores) had the shallowest depth of occurrence in the diets of both predator species. Annelids (the most common prey items for both species) were consumed by both species at stations with fine sand (low PC2 score). The PCA plot (Fig. 5) also reflects some separation in foraging niche (including prey species and foraging habitat characteristics) between species: yellowfin sole consumed bivalves at relatively shallow, muddy stations, in comparison with the stations where this species consumed other prey. In contrast, northern rock sole consumed bivalves at deeper, sandier stations. Cnidaria (anemone tentacles) were not a common prey item of either species, but their high PC2 score indicates their consumption by yellowfin sole in areas with large grain sediments.

Discussion

Many flatfish species rely upon juvenile nursery habitats in shallow, coastal areas whose spatial extent is markedly smaller than that of adult distribution (Gibson, 2005). As such, flatfishes are considered particularly prone to density-dependent growth and recruitment limitations associated with interspecific competition for habitats and prey ("space concentration hypothesis;" Beverton, 1995). Furthermore, these coastal nurseries are commonly inhabited by multiple flatfish species, indicating the potential for interspecific competition and density dependence (Vinagre et al., 2005; Mariani et al., 2011). Consequently, numerous studies have examined the patterns of niche overlap and partitioning with regard to habitat associations and foraging of juvenile flatfishes (e.g., Carter et al., 1991; Vinagre et al., 2005; Tomiyama and Omori, 2008; Mariani et al., 2011). In this study, we examined the foraging habits and dietary overlap of juvenile yellowfin sole and northern rock sole in previously uncharacterized nearshore bays in the SEBS and examined functional differences in the foraging habits of these species. These observations indicate that direct competition for prey resources between juveniles of these co-occurring species is reduced by a combination of differential habitat associations and prey selection. However, this differentiation indicates that climate change in the SEBS may differentially affect the forage base and productivity of these species.

The diets of juvenile yellowfin sole and northern rock sole captured along the Alaska Peninsula of the SEBS in our study were generally similar to observations in other parts of the ranges of these species. Both species are generalist benthic invertebrate predators, with polychaetes and amphipods generally dominating their diets (Corcobado Oñnate, 1991; Holladay and Norcross, 1995; Lang et al., 1995; Hurst et al., 2007; Yeung and Yang, 2017). The incorporation of secondary diet components varied across studies. For example, bivalves were rare in the diets of both species in our sampling area, common in the diets of yellowfin sole (but not in those of northern rock sole) in broader sampling of the Bering Sea, (Lang et al., 1995), and common in diets of northern rock sole (but not in those of yellowfin sole) in coastal waters of the GOA (Holladay and Norcross, 1995; Hurst et al., 2007).

The largest difference between diets of yellowfin sole and northern rock sole was the higher occurrence of mysids and euphausiids in the diets of northern rock sole. These taxa composed >40% (by weight) of the diets of northern rock sole but were only minor components (by weight) of the diets of yellowfin sole (mysids: 7%; euphausiids: 1%). Mysids and euphausiids appear to be consistently rare in the diets of juvenile yellowfin sole, with no indication of a significant contribution reported from previous studies. The incorporation of these taxa in the diets of northern rock sole appears more variable across studies, potentially varying over space and time. Mysids were rare in 2 previous studies in the SEBS (Lang et al., 1995; Yeung and Yang, 2017). Mysids were important in the diets of juvenile northern rock sole in one GOA study (Holladay and Norcross, 1995) but not in another (Hurst et al., 2007). Interestingly, in both studies in the GOA, mysids were the dominant prey of juveniles of other co-occurring flatfishes, indicating that their rarity in the diets of northern rock sole and yellowfin sole is a reflection of prey selection as opposed to availability.

The consumption of euphausiids by northern rock sole observed in our study appears to be greater than that observed in previous studies of similarly sized northern rock sole. Because euphausiids are highly aggregated, pelagic prey that undertake diel vertical migrations (Schabetsberger et al., 2000), it is possible that the conditions under which northern rock sole consume them are more limited than those for consumption of other types of prey.

Dietary niche partitioning

In waters of Alaska, yellowfin sole and northern rock sole have overlapping distributions at both the juvenile and adult stages and have been the most abundant fish species in our sampling area (Hurst, 2016). The degree of dietary overlap is an important indicator of the potential for interspecific competition between species in their juvenile nurseries. Lang et al. (1995) found high dietary overlap and potential competition between juvenile yellowfin sole and northern rock sole (fish <200 mm SL in depths <50 m: SI=0.70). Across our study area, the dietary overlap of these species was low (SI=0.39). The differential consumption of mysids and euphausiids contributed to the low levels of dietary overlap in our study and is likely facilitated by morphological differences between the 2 species (Barnes et al., 2021). Although flatfishes share broadly similar body morphologies, variations between species are associated with specific foraging habits (Livingston, 1987, Russo et al., 2008). Of the 2 species we studied, the northern rock sole has the more extendable jaw and a narrower field of vision, both characteristics that favor the consumption of more mobile prey (Lang et al., 1995).

The dietary niche partitioning between the species, indicated by the low overall SI values across the sampling area, was also in part due to fine-scale habitat segregation (Mariani et al., 2011). Although both species were widespread in the study area, northern rock sole were in deeper, colder water than yellowfin sole (Hurst, 2016). In this study, the overlap coefficient was notably higher (SI=0.55) when calculated by using only fish collected at sampling locations where the species co-occurred. Interestingly, the opposite pattern was observed in coastal embayments in the GOA: dietary overlap was lower at stations where these species co-occurred than across all stations in the study area (Holladay and Norcross, 1995).

Dietary overlap indicates the potential for competitive interactions between species, but index values should be interpreted with caution. Dietary overlap may occur between species because of the shared utilization of locally abundant resources as opposed to competition for a limited resource (Carter et al., 1991). Alternatively, when species have niche separation (i.e., low dietary overlap), it can be difficult to determine if the low overlap reflects differences in habitat preferences with diets reflecting availability of prey or vice versa (i.e., consumers occupy habitats because of the availability of preferred prey). The novel approach to application of PCA to multi-species diet composition data in our study provided additional insight into foraging dynamics of the northern rock sole and yellowfin sole. This analysis included both the biotic traits of the consumer (size and Fulton's condition factor) and the abiotic aspects of their environment (depth, temperature, and sediment characteristics). The general separation between these predator species along the first axis of the PCA illustrates the difference in overall foraging habitats, with northern rock sole consuming prey in deeper waters, with more sandy sediments, and at later times of day in comparison to the diets of yellowfin sole. The separation also indicates that certain prey were predominantly consumed in specific habitats. In particular, euphausiids were consumed in deeper water than other prey by both species; whereas, hyperbenthic copepods were consumed by both species in shallow waters.

Foraging patterns and predation risk

Flatfishes possess a unique combination of morphological and behavioral adaptations associated with their demersal lifestyle. These traits indicate that avoiding detection by predators is critical to the survival of juvenile flatfish. For flatfish species, foraging activity likely directly conflicts with anti-predator behaviors that reduce conspicuousness. This trade-off is expected to be even greater when flatfish leave the sediment surface to forage in the water column because of the exposure of their unpigmented (and highly conspicuous) blind side (Hurst and Duffy, 2005). However, even within this guild, there are differences among species in behavioral characteristics.

In earlier studies that compared life history strategies of 3 co-occurring flatfishes, northern rock sole were considered the most "risk averse" in that they maintained the lowest body profile on the sediment surface and had the lowest activity rates (Lemke and Ryer, 2006). Consistent with the finding of this risk-averse lifestyle, laboratory and field observations indicate that foraging (Corcobado Oñate, 1991; Hurst et al., 2007) and overall activity of northern rock sole were greatest during dusk periods (Hurst and Duffy, 2005). Although sampling during this study was conducted only during daylight hours, northern rock sole had a temporally restricted feeding pattern consistent with that observed in those previous studies.

Comparatively little work has been conducted on the behavioral ecology of juvenile yellowfin sole. However, several pieces of evidence indicate that their strategy may be even more risk averse than that of northern rock sole. Yellowfin sole consumed less hyperbenthic and pelagic prey whose capture presumably would entail risky off-bottom swimming. In addition, Hurst (2016) found juvenile yellowfin sole at shallower depths than northern rock sole, indicating reduced encounters with large-bodied predators, as articulated in the shallow-water refuge hypothesis (Paterson and Whitfield, 2000; Linehan et al., 2001).

Conclusions

The coexistence of yellowfin sole and northern rock sole on shared nursery grounds is likely facilitated by aspects of niche separation along habitat and dietary preferences. Yellowfin sole appear to be obligate benthic foragers with narrower diets than those of northern rock sole, indicating a greater sensitivity to environmentally driven changes in availability of demersal infauna and epifauna (Poiesz et al., 2020). These differences also indicate that these species may respond differently to environmental change. Because our sampling was conducted in a comparatively cold year (in 2012) in a rapidly warming ocean region (Stabeno et al., 2017), the data from our study serve as a useful baseline for evaluating effects of climate on food-web interactions in the SEBS. In addition to dietary differences between the 2 species, growth rates of yellowfin sole appear more sensitive to temperature variation than those of northern rock sole (Matta et al., 2010; T. Hurst, unpubl. data). Interestingly, the distribution of juvenile yellowfin sole appears to be more stable in the face of fluctuating environmental conditions than that of northern rock sole (Yeung and Cooper, 2020). This combination of narrower diet breadth, greater thermal sensitivity, and stable distribution may result in stronger environmental sensitivity in the productivity of yellowfin sole in the future.

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Validation of methods for aging goosefish (*Lophius americanus*) based on length-mode progression of a strong cohort

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Abstract—An unusually strong year class of goosefish (*Lophius americanus*) was first observed in the spring of 2015, and the length mode for this particular cohort remained evident for several years. We collected monthly samples from within this length mode over a period of 3 years and considered them fish with known ages for validating ages estimated by using illicia and vertebrae. Recent research had found vertebral ages for goosefish to be inaccurate, and a method in which illicia are used for *Lophius* species in Europe seemed promising. However, ring counts from illicia matched the known age only 50% of the time and were not replicable (9% agreement). Ring counts from vertebrae never matched the known age but were replicable in 68% of samples. Marginal increment analysis of illicia from fish that matched the known age provided evidence that one annulus is formed on the illicium in spring or summer of each year for fish aged from 1 to 2 years. Because of the low accuracy of age estimates made with both illicia and vertebrae, as well as the high bias of aging with vertebrae, we concluded that the methods based on these structures did not provide useful age estimates of goosefish. The observed growth rate, based on the progression of the length mode during our study, was much faster than the growth rates based on vertebral ages.

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The goosefish (*Lophius americanus*) is one of the most economically important fish species of the continental shelf off the northeastern United States. This species has been managed conservatively because of major uncertainties in stock assessment (NDPSWG, 2007; Haring and Maguire, 2008). One of the most significant uncertainties is the growth curve, which has been viewed with caution (NDPSWG, 2007) because it appears linear rather than asymptotic (Richards et al., 2008).

The growth curve for goosefish is based on ages derived from vertebrae, with an aging method that was used at the NOAA Northeast Fisheries Science Center (NEFSC) during 1998–2007. Age estimation efforts at the NEFSC were suspended in 2007, because of concerns raised at a stock assessment review (NDPSWG, 2007). The structures normally used to estimate ages for other fish species (e.g., scales and sagittal otoliths) cannot be used for goosefish because they lack scales and because sagittal otoliths are not reliable structures for aging this species (Armstrong et al., 1992; Hartley, 1995).

The vertebral method was described by Armstrong et al. (1992), who examined marginal increment widths on vertebrae and concluded that rings were formed in May of each year. Results from Armstrong et al. (1992) indicate that vertebrae met the minimal criteria for use as an aging structure (Van Oosten, 1928). However, direct validation of the vertebral aging method had not been undertaken, perhaps because goosefish have very poor survival in captivity (Richards et al., 2011). Recently, Bank et al. (2020) successfully completed a direct age validation study that involved chemical marking of wild and laboratory-maintained goosefish. They demonstrated that the vertebral aging method was accurate less than 50% of the time for fish up to 2.4 years after tagging. However, results of their preliminary examination indicate that use of illicia (first spines on the dorsal fin) might provide more reliable age estimates. Illicia are the primary structures used to age white anglerfish (*L. piscatorius*) and black anglerfish (*L. budegassa*) in Europe (Duarte et al.[1]; Fariña et al., 2008; Landa et al., 2013).

An opportunity for further age validation work was presented by an exceptionally strong recruitment event for goosefish that occurred along the Atlantic coast of the United States in 2015. Recruitment indices in June 2015 were nearly an order of magnitude higher than long-term averages (Richards, 2016), with a modal length encompassing the size at settlement (Able et al., 2007). This clearly defined length mode remained evident for several years, providing a natural tag for identifying samples with known ages.

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[1] Duarte, R., J. Landa, I. Quincoces, H. Dupouy, E. Bilbao, J. Dimeet, A. Marçal, H. McCormick, and G. Ni Chonchuir. 2002. Anglerfish ageing guide, 40 p. Working document of the 4th international ageing workshop on European anglerfish; Lisbon, 14–18 January. [Available from website.]

We collected samples from the 2015 year class of goosefish at ages of 1–3 years as the foundation for an age validation study focused on examining both illicia and vertebrae. Our goals were 1) to confirm year-class membership of our samples, 2) to determine if ages estimated from illicia and vertebrae were accurate, 3) to evaluate the precision of age estimates from the use of these structures, and 4) to determine the timing of annulus formation on illicia. In addition, we estimated growth rates for fish 1–3 years old.

Materials and methods

Length composition from surveys

Goosefish were captured and measured during annual fishery-independent surveys conducted by the NEFSC along the Atlantic coast of the United States from Virginia to Georges Bank (Fig. 1). These surveys included the NEFSC bottom trawl surveys (Stauffer, 2004), conducted in spring and autumn, and the NEFSC and Virginia Institute of Marine Sciences scallop dredge survey (NEFSC, 2010), conducted each June.

The length distribution of goosefish in surveys between June 2015 (when the strong year class was first observed in catches) through September 2018 was examined. At each survey time step, length at age was estimated by fitting normal curves to the dominant length mode (stratified mean number per tow at length) presumed to represent the

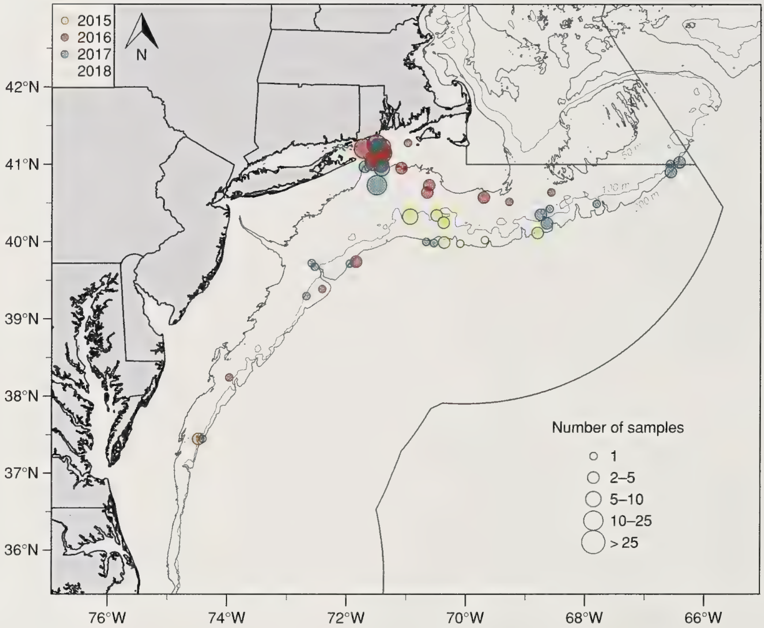

Figure 1

Map of sampling locations along the Atlantic coast of the United States from Virginia to Georges Bank where goosefish (*Lophius americanus*) were collected for this study from September 2015 through April 2018. Samples were obtained from the Northeast Fisheries Science Center (NEFSC) bottom trawl surveys, the NEFSC and Virginia Institute of Marine Science scallop dredge survey, the NEFSC Study Fleet, and the NEFSC Fisheries Monitoring Operations Branch. Circle color indicates the year of collection, and circle size indicates the number of samples.

2015 year class. Normal parameters were estimated by using NORMSEP software, a program for analyzing a mixture of normal distributions (Pauly et al., 1986; Gayanilo et al., 2005). The size estimates of the length mode for each month were later used to select samples from within the mode for the validation study.

Sample collection

Samples of the 2015 year class (with determination of year class based on fish length, as described here previously) were obtained from the Atlantic coast of the United States from Virginia to Georges Bank (Fig. 1). Sampling occurred during the NEFSC bottom trawl surveys in 2016–2018 (spring survey) and 2015–2016 (autumn survey) and during the NEFSC and Virginia Institute of Marine Sciences scallop dredge survey in June 2016. To obtain samples in months when no surveys occurred, additional samples were obtained through the NEFSC Study Fleet program (Palmer et al., 2007) and the NEFSC Fisheries Monitoring Operations Branch (NEFSC[2]). The overall sampling effort spanned from September 2015 through April 2018, although monthly sampling was limited to the period from May 2016 through July 2017.

All fish were frozen whole and shipped to the laboratory for dissection. Each fish was measured (in total length [TL] in centimeters), weighed (in grams), and examined macroscopically to determine sex. The illicium and a segment of the vertebral column were removed.

Hatch date

In order to verify year-class membership of fish in the strong length mode, we additionally removed the lapillar otoliths from 2 presumed young-of-the-year goosefish from within this length mode by using methods described in Landa et al.[3] These fish were fortuitously collected on 4 September 2015, before our dedicated sampling began.

The lapillar otoliths were prepared for daily aging following methods described in Secor et al. (1991) and Wright et al. (2002). Each otolith was mounted in epoxy, sectioned along the sagittal plane, manually ground (240- and 600-grit sandpaper) to reveal the primordium, and polished.

Images of the lapillar otolith sections were taken at 125× magnification with an Olympus[4] BX60 microscope, Olympus DP70 camera, and imaging software cellSens, vers. 1.11 (Olympus Corp., Tokyo, Japan). One age reader used the images to count the rings (Fig. 2) from the primordium to the outer edge, with replicate counts on 3 successive days (this reader trained with D. Secor, of the University of Maryland Center for Environmental Science, Solomons, MD, to learn methods for processing and reading samples for daily aging). It was assumed that the first ring was formed at hatching and that each ring represented 1 d of growth (Hislop et al., 2001; Hernández et al., 2015). Provided that the 3 readings were within 10% of each other, the average of the 3 counts was used to calculate hatch date (the collection date minus the number of rings).

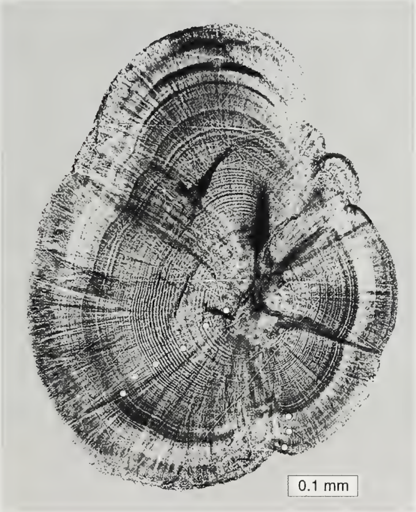

Figure 2

Photograph of a sectioned and ground lapillar otolith of a 14-cm-TL goosefish (*Lophius americanus*) captured on the outer shelf off the coast of Virginia on 4 September 2015. The estimated hatch date is 4 June 2015. The white dots indicate every tenth ring.

Age estimation

Illicia were prepared according to methods described in Duarte et al.[1] Each illicium was skinned and cleaned, marked 0.5 cm above the top of the basal bulb, and allowed to dry. The illicia were then mounted in polyester resin, with 10–15 samples per row, and sectioned at the mark on a high-speed saw with a diamond-impregnated blade (LabCut 250, Benetec Ltd., Rugby, UK) to a thickness of 0.5 mm.

Vertebrae were processed according to methods established by Armstrong et al. (1992) but were not sectioned. The eighth vertebra was excised from the spinal column, cleaned of tissue, and baked at 230°C in an oven until dried and darkened (20–60 min).

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[2] NEFSC (Northeast Fisheries Science Center). 2016. Observer operations manual, 163 p. Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., Woods Hole, MA. [Available from website.]

[3] Landa, J., A. Antolínez, J. Barrado, J. Fontenla, C. Hernández, B. Villamor, C. Dueñas, and M. R. Navarro. 2014. Age determination procedures for benthic fish in Spanish Institute of Oceanography (IEO), 34 p. Int. Doc., Inst. Esp. Oceanogr., Santander, Spain. [Available from website.]

[4] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

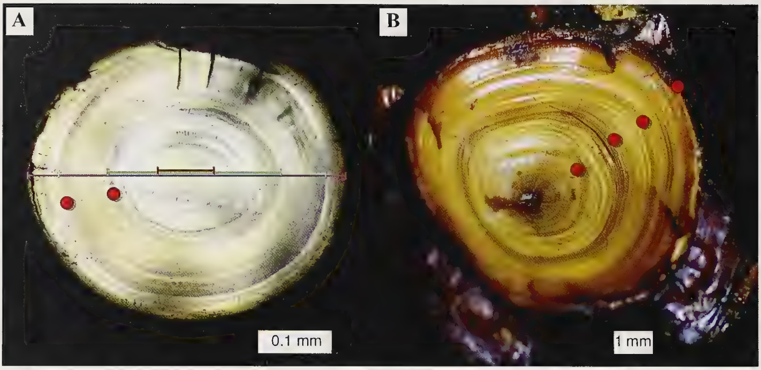

Figure 3

Annotated images of age structures, (**A**) an illicium section and (**B**) a baked vertebra, taken from a 41-cm-TL goosefish (*Lophius americanus*) with a known age of 2 years that was captured on 9 April 2017 south of Rhode Island. Each ring is marked with a red dot. The image of the illicium section shows 2 rings and the following measured diameters: settling check (red), first ring (green), last ring (blue), and total (pink). The image of the vertebra shows 4 rings.

Rings on each structure were counted twice following NEFSC aging protocols (Penttila and Dery, 1988) by one age reader, with at least 2 weeks between readings. Data on month, but not year, of capture were available to the age reader. Any samples for which the 2 ring counts differed were reexamined later; samples for which the count still could not be resolved were excluded from the analysis.

The reading order of rows of illicia (10–15 samples per row) was randomized before samples were examined. Vertebral samples were viewed in a haphazard order, by mixing together the envelopes that held the samples and viewing the samples in the order they were pulled out of a box.

The reader had over 15 years of experience with age reading methods, including the vertebral method for aging goosefish. However, the reader had examined fewer than 200 illicia prior to this study. Immediately before examining the study samples, the reader reviewed a set of 24 images of illicia from goosefish that had been examined and annotated by another age reader (Landa[5]) experienced with illicia from anglerfish sampled in Europe.

Sectioned illicia (Fig. 3A) were immersed in a 1:1 solution of glycerin and 70% isopropyl alcohol and were viewed with transmitted light at 40× magnification on an Olympus BH2 compound microscope (Olympus Corp.). Recommended practices for viewing illicia of white anglerfish (Duarte et al.[1]; Landa et al., 2013) were followed, including adjusting lighting and focus, counting the dark rings, and using axes with greater color contrast. It was assumed that the first ring would be nearly circular and that it would be outside both an oval settling check and a false annulus (as has been observed in white anglerfish by Wright et al., 2002). This process yielded first rings comparable in diameter to those in the annotated images.

Vertebrae (Fig. 3B) were interpreted following the methods of Armstrong et al. (1992). Samples were viewed with reflected light at 10× magnification on a dissecting microscope (Leica MZ6, Leica Camera AG, Wetzlar, Germany).

After both structures from all fish had been assigned a final ring count, accuracy of readings (ring counts versus known ages) for each structure was calculated across all fish. Known ages were based on the calendar year of capture (i.e., a fish captured in 2016 had a known age of 1 year). Later, test counts were made on a random subset of samples for each structure, allowing intra-reader precision (test counts versus ring counts) to be estimated.

Statistics calculated for each of these measures were percent agreement and the mean coefficient of variation (CV) (Chang, 1982). For both precision tests, a Bowker's test of symmetry (Bowker, 1948; Hoenig et al., 1995) was additionally applied to test for bias in the paired ring counts (one count each from the initial and the test count for a given structure of a sampled fish). At the NEFSC aging laboratory, 80% is considered an acceptable level of agreement; an acceptable CV is under 5% (NEFSC[6]).

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[5] Landa, J. 2016. Personal commun. Cent. Oceanogr. Santander, Inst. Esp. Oceanogr., Promontorio San Martín s/n, 39004 Santander, Cantabria, Spain.

[6] NEFSC (Northeast Fisheries Science Center). n.d. Quality assurance and quality control estimates for the production ageing of northwest Atlantic species: statistical measures. [Available from website, accessed November 2021.]

Marginal increment analysis

Marginal increment analysis was conducted only for illicia because it had been done previously for vertebrae (Armstrong et al., 1992). Samples were limited to those collected during May 2016–May 2017 and for which the ring count matched the known age. Furthermore, only samples that had at least one band inside the edge (i.e., a minimum age of 1+; the notation 1+ indicates the presence of additional material outside the first ring) were included because relative increment width cannot be calculated on younger fish, whose illicia lack rings inside the edge.

Illicia were imaged and measured with knowledge of known age but without knowledge of fish length or capture date. The order in which they were examined was randomized by row. Images were taken at 150× magnification with an Olympus BH2 microscope, an Olympus DP25 camera (Olympus Corp.), and 64-bit TWAIN Twacker software (vers. 2.0; TWG, 2008). ImageJ software (vers. 1.49v; Schneider et al., 2012) and the ObjectJ plugin (vers. 1.03s; University of Amsterdam, available from website) were used for image processing.

Diameters of the settlement check, first ring, last ring inside the edge (R_n), and total illicium diameter (D) were measured to the nearest 0.0001 mm along the axis with the largest settlement check diameter (Fig. 3A). Relationships between these measurements (settlement check, first ring, and total diameter) and total length were examined by using linear regression on untransformed data with the regression analysis add-in for Microsoft Excel 2016 (Microsoft Corp., Redmond, WA). Regression results were used to test the assumption that the diameters of the settling check and first annulus were constant across the range of fish lengths. Total illicium diameter was expected to increase linearly with fish length.

These measurements were then used to calculate the relative marginal increment (MIR) (Sun et al., 2002):

$$MIR = \frac{D - R_n}{R_n - R_{n-1}}, \tag{1}$$

where R_{n-1} = the penultimate ring.

If the last ring is on the edge, $D-R_n=0$. For fish with only one ring inside the edge (i.e., fish with estimated ages of 1+ or 2 years), R_{n-1} is not present, simplifying the calculation to the following equation (Vilizzi and Walker, 1999):

$$MIR = \frac{D - R_n}{R_n}. \tag{2}$$

Average MIR was calculated for each month, and minima in the monthly MIR values were considered indicative of the timing of ring deposition.

Results

Survey length composition and sample collection

The length mode representing the 2015 year class (Table 1, Fig. 4) was first seen in the scallop dredge

Table 1

Known age, mean length with standard deviation (SD), and growth increment of the dominant length mode of goosefish (*Lophius americanus*) collected during surveys conducted by the NOAA Northeast Fisheries Science Center from June 2015 through September 2018 along the Atlantic coast of the United States from Virginia to Georges Bank. Mean length was estimated by using normal curves fit to the stratified mean number per tow at length. Growth increment was calculated as the change in length divided by the number of days since the previous survey. Surveys include bottom trawl surveys conducted in spring and autumn and scallop dredge surveys conducted each June. TL=total length.

Survey	Average survey date	Known age (years)	Fractional age (years)	Mean length (SD) (cm TL)	Growth increment (cm TL/d)
Scallop 2015	7-Jun-2015	0	0.0	10.7 (1.8)	
Autumn 2015	20-Sep-2015	0	0.3	21.6 (3.5)	0.10
Spring 2016	1-May-2016	1	0.9	27.2 (3.6)	0.03
Scallop 2016	29-May-2016	1	1.0	26.2 (3.8)	−0.04
Autumn 2016	27-Sep-2016	1	1.3	36.8 (3.7)	0.09
Spring 2017	2-Apr-2017	2	1.8	40.9 (4.2)	0.02
Scallop 2017	11-Jun-2017	2	2.0	41.7 (6.2)	0.01
Autumn 2017	25-Oct-2017	2	2.4	51.5 (6.4)	0.07
Spring 2018	7-Apr-2018	3	2.9	50.7 (8.1)	0.00
Scallop 2018	1-Jun-2018	3	3.0	53.0 (6.7)	0.04
Autumn 2018	22-Sep-2018	3	3.3	53.0 (6.1)	0.00

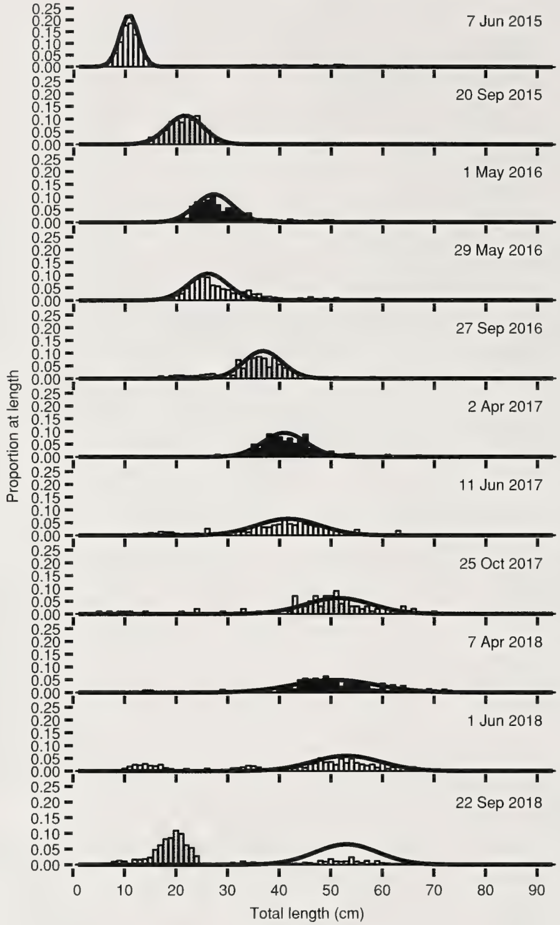

Figure 4

Length–frequency distributions of goosefish (*Lophius americanus*) from the 2015 year class captured along the Atlantic coast of the United States from Virginia to Georges Bank between June 2015 and September 2018 during scallop dredge (white bars) and autumn (gray bars) and spring (black bars) bottom trawl surveys conducted by the NOAA Northeast Fisheries Science Center. The graphs illustrate the length progression of the 2015 year class. Dates indicate the average date of each survey, and curved lines represent the normal curves that were fit to stratified mean number per tow at length for the year class during each survey.

survey conducted in 2015 (average date: 7 June 2015) and was visible in survey catches through the autumn of 2018. Between September 2015 and April 2018, 204 fish were collected from this length mode as it grew (Table 2, Fig. 1).

Figure 4 shows a new year class entering the population in 2018. This 2018 year class had a modal length of approximately 14 cm TL in early June and a length of 20 cm TL by September. These lengths are similar to the lengths of the 2015 year class at age 0 during the same times of year (11 and 22 cm TL, respectively; Table 1).

Hatch date

Individual counts of daily rings averaged 91.7 and 99.3 for the 2 fish caught on 4 September 2015. There was less than a 5% difference between the minimum and maximum counts from each fish (ranges: 90–94 rings and 96–101 rings). The estimated hatch dates were 28 May 2015 and 4 June 2015. The average growth rate (from the estimated hatch date until the date of collection) was 1.52 mm/d for both fish.

Age estimation

Ring counts were assigned to 190 illicia and 203 vertebrae (Suppl. Table) (online only). Ring counts could not be assigned to 14 illicia because of missing or broken structures (5 fish), processing problems (8 fish), or failure to reach a consensus (1 fish). For readings of vertebrae, no fish were omitted because of processing or aging issues (the spinal column was not collected for one of the fish sampled in September 2015).

Accuracy of ring counts from illicia was 50.0%, with a CV of 20.0% (number of samples [*n*]=190) (Fig. 5A). Where disagreements occurred, the ring count was always higher than the known age. In contrast, accuracy of ring counts from vertebrae had 0% agreement with the known age and a CV of 69.5% (*n*=203) (Fig. 5B). All vertebral ring counts were higher than known ages (98% exceeded known age by 2–3 years), with increasing error for higher known ages.

Precision of ring counts from both structures was low. Agreement between repeated readings of illicia was only 8.8% (CV=44.6%, *n*=57) (Fig. 6A), with a strong bias toward higher counts in the test set (Bowker's test: $P<0.001$). Agreement between readings from vertebrae was 67.9% (CV=5.9%, *n*=56) (Fig. 6B).

Table 2

Details for samples of goosefish (*Lophius americanus*) collected from June 2015 through September 2018 along the Atlantic coast of the United States from Virginia to Georges Bank and used in this study. Sources of samples include surveys of the NOAA Northeast Fisheries Science Center (NEFSC), the NEFSC Study Fleet program, and the NEFSC Fisheries Monitoring Operations Branch (FMOB). SD=standard deviation; TL=total length.

Year	Month	Known age (years)	No. of samples NEFSC surveys	Study Fleet	FMOB	Total no. of samples	Mean length (SD) (cm TL)
2015	September	0	2			2	14.5 (0.7)
2016	May	1	3			3	28.0
	June	1	1	18	36	55	29.7 (3.9)
	July	1		11		11	33.5 (1.9)
	August	1		15		15	36.7 (2.1)
	September	1	12	9		21	34.0 (2.9)
	October	1		11		11	36.8 (2.3)
	November	1		9		9	38.6 (1.9)
	December	1		10		10	37.2 (1.5)
2017	January	2		6		6	37.2 (0.8)
	February	2		13		13	37.8 (1.6)
	March	2	6			6	40.3 (2.1)
	April	2	12	2		14	42.0 (2.0)
	May	2		5		5	44.8 (1.9)
	July	2		3		3	42.7 (0.6)
2018	April	3	20			20	51.8 (3.6)
Total			56	112	36	204	

Marginal increment analysis

A total of 74 illicia were examined in the marginal increment analysis, including 61 illicia that had only one ring inside the edge (ages from 1+ to 2 years). The narrowest MIR widths were measured in illicia from fish sampled in May–July 2016 and in April 2017; maximum MIR widths were measured in illicia from fish sampled in December 2016 (Fig. 7). Monthly sample sizes ranged from 1 to 12 fish.

Diameters of various marks in illicia were compared against fish length (Fig. 8). The mean diameter of the settlement check was 0.078 mm (95% confidence interval [CI]: 0.075–0.081 mm); the diameter of the settling check increased with fish length (linear regression: slope=0.0005, P=0.04, coefficient of determination [r^2]=0.05). The first ring was visible inside the edge in fish as small as 24–28 cm TL and had a mean diameter of 0.259 mm (95% CI: 0.253–0.265 mm); the diameter of the first ring increased with fish length (linear regression: slope=0.0017, P=0.0005, r^2=0.12). Illicium diameter increased linearly with fish length (linear regression: r^2=0.85).

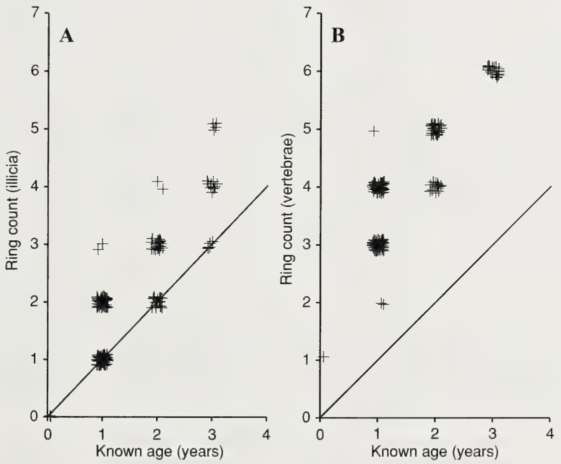

Figure 5

Accuracy of ring counts versus known ages from readings of (**A**) illicia and (**B**) vertebrae of goosefish (*Lophius americanus*) captured along the Atlantic coast from Virginia to Georges Bank between September 2015 and April 2018. The diagonal lines represent equivalence. Points have been jittered to improve the visibility of overlapping data.

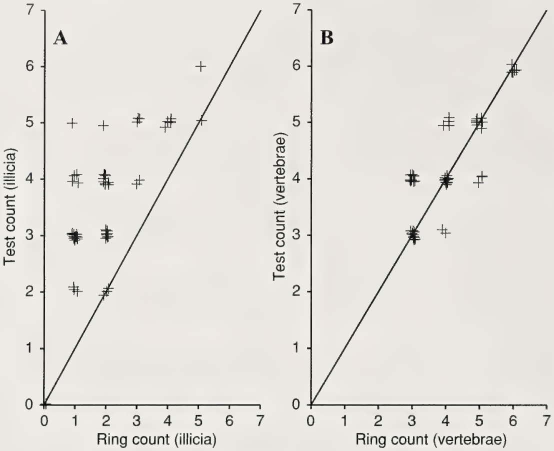

Figure 6

Precision of ring counts, indicated by the relationship between test and original counts from readings of (**A**) illicia and (**B**) vertebrae of goosefish (*Lophius americanus*) captured along the Atlantic coast from Virginia to Georges Bank between September 2015 and April 2018. The diagonal lines represent equivalence. Points have been jittered to improve the visibility of overlapping data.

Growth

Goosefish in the 2015 year class reached a modal length of 26 cm TL by the end of their first year of life (in May 2016) (Table 1, Fig. 9) and increased to 42 cm TL a year later (growth of 16 cm TL in that year). Growth slowed thereafter, with a modal length of 53 cm TL at 3 years (growth of 11 cm TL in the third year). Growth was most rapid between June and September–October.

Discussion

We used a strong recruitment event as a source of fish with known ages in order to validate the use of 2 aging structures for goosefish. Previous studies (Jónsson[7]; Landa et al., 2013) of white anglerfish have also tracked abundant cohorts across multiple years to test aging methods. Those studies successfully confirmed that the illicium is an appropriate aging structure for white anglerfish; however, we were not able to validate use of illicia for aging goosefish.

The dominant length mode of the 2015 year class of goosefish was first observed in June 2015 and remained distinct for more than 3 years (Fig. 4). Results from daily aging of 2 fish that were fortuitously collected in the autumn of 2015 confirm that fish in the length mode were members of the 2015 year class. Therefore, we were confident that fish sampled from within this length mode were hatched in 2015 and could be assigned known ages based on this hatch year.

In assigning known ages, we assumed that potential confounding issues (Campana, 2001), such as size-selective mortality, migration, and multiple recruitment events, were not factors in our study. However, all of these issues could have played a role. For example, size-selective mortality could either increase apparent growth rates if the smallest fish are removed by predation or decrease apparent growth rates if the largest, fastest-growing fish are removed through fishing. The 2015 year class had attained exploitable size by June 2017 and was subject to discarding in 2016 (NEFSC, 2020); therefore we may have underestimated size at ages 1–3. The length modes remained distinct, however, and assignment of known age was unlikely to have been biased by size-selective mortality. Female goosefish can spawn more than once per year (Johnson et al., 2008; McBride et al., 2017), possibly creating a bimodal length distribution within a year class. Still, there is no indication of multimodality in the size composition of the age-0 mode (Fig. 4). Migratory movements may also create checks on an age structure, given that a fish may move between temperature regimes. Goosefish make seasonal inshore–offshore movements (Richards et al., 2008; Rountree et al., 2008), and evidence indicates that some fish make latitudinal movements (Cadrin et al.[8]; Cadrin and Bank[9]). Results from tagging studies of white anglerfish indicate some migrations of very long distances (Laurenson et al., 2005), as well as more frequent seasonal movements (Laurenson et al., 2005; Ofstad, 2013). We were unable to evaluate the potential effects of migration on our results.

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[7] Jónsson, E. 2007. Verification of anglerfish (*Lophius piscatorius*) age estimation through comparison of length modes of age read fish (illicia) to length modes of large year-classes appearing in the Icelandic stock. ICES CM 2007/K:03, 17 p. [Available from website.]

[8] Cadrin S. X, C. Bank, J. H. Grabowski, and G. Sherwood. 2017. Archival tagging and age validation in the mid-Atlantic, 51 p. 2014 monkfish RSA. Project completion report. NOAA grant no. NA14NMF4540227. Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., Woods Hole, MA. [Available from website.]

[9] Cadrin, S., and C. Bank. 2019. Estimating growth and movement of juvenile monkfish, 18 p. Final project report. Award no. NA16NMF4540108. Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., Woods Hole, MA. [Available from website.]

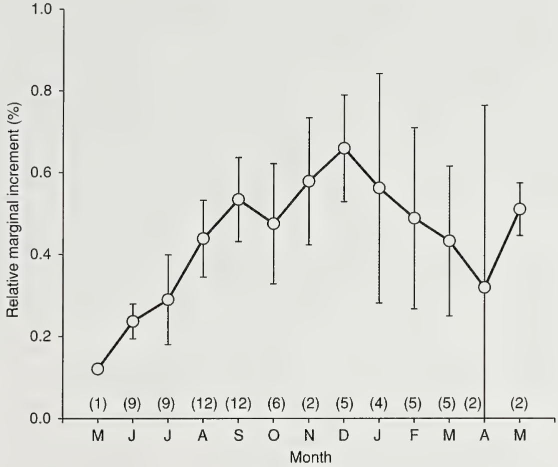

Figure 7

Average relative marginal increment on illicia by month for goosefish (*Lophius americanus*) captured along the Atlantic coast from Virginia to Georges Bank during May 2016–May 2017. Numerals in parentheses along the x-axis indicate monthly number of samples. Error bars indicate 95% confidence intervals.

Hatch date

The average hatch date, 1 June 2015, supports our assumption that fish in the strong length mode were hatched in 2015. This spawning date is consistent with other survey observations and studies of goosefish biology. The strong 2015 recruitment was first observed in the scallop dredge survey conducted in early June 2015 (Fig. 4) but was not observed in the NEFSC bottom trawl survey that took place about 2 months earlier in the same region. This finding indicates that settlement occurred sometime between early April and early June. The similarity between the lengths of the modes representing the 2015 and 2018 year classes in June and September of those years implies that the 2015 year class was growing in a typical way. Able et al. (2007) observed that goosefish settle to the benthos at lengths of about 7 cm TL (range: 5–8 cm TL), a size that approximates the lower bound of the length mode we observed in June 2015 (Fig. 4).

Results of additional studies of goosefish biology also support our interpretation that the strong length mode was composed of fish hatched in 2015. Goosefish along the Atlantic coast of the United States from Virginia to Georges Bank spawn from late winter through summer (Johnson et al., 2008; McBride et al., 2017). Hatching occurs from June through October with a peak in July (Able et al., 2007), larval abundance peaks in May–June (Able et al., 2007; McBride et al., 2017), and juveniles settle to the benthos 5–10 weeks after hatching (Able et al., 2007). Therefore, although our sample size for estimating hatch date was small, our results are consistent with expectations from many additional lines of evidence.

Age estimation

Illicium diameter increased with fish length (Fig. 8), indicating that this structure continues to accrete, one of the characteristics of a structure that is effective for age determination (Van Oosten, 1928). The diameters of both the settlement check and the first ring point to a weak positive relationship with fish length, indicating that the internal portions of the illicium may have changed as the fish grew or that the marks may not have been identified consistently. However, in our study, this change was minimal, as there was little variation in these diameters across all the samples, and the values were similar to those obtained from larger fish (>50 cm TL) (Bank et al., 2020). Ofstad et al. (2013) also noted changes in the size of the first ring in samples of fish under 50 cm TL.

Bank et al. (2020) suggested that the illicium might prove to be a useful structure for aging of goosefish because they had greater success with illicia than with vertebrae in finding the winter increments after the chemical mark. They also described how recent advances in preparation and interpretation of illicia may have made age interpretation easier for this structure. However, we did not find the expected number of rings on illicia in 50% of samples (Fig. 5A), and precision was only 9% (Fig. 6A). These levels of accuracy and precision are not adequate for age estimation. Ring counts from illicia tend to overestimate age. The bias is not consistent, precluding use of a standard correction.

Although studies on other *Lophius* species have been able to validate yearly marks on illicia (Jónsson[7]; Landa et al., 2013), the structure remains a challenge to read (Duarte et al.[1]; Landa et al., 2013). Many rings are visible, and it is difficult to choose which ones to count. Unlike with typical aging structures, the spacing between annuli does not decrease with age and is consistent across the section; increment width may even increase near the edge (Duarte et al.[1]). Disagreements between otolith- and illicium-derived ages of white anglerfish were not resolved until Wright et al. (2002) showed that an additional ring (i.e., false annulus) is formed on illicia. However, it is possible that goosefish illicia may have multiple false annuli. This complexity in reading illicia may also account for the

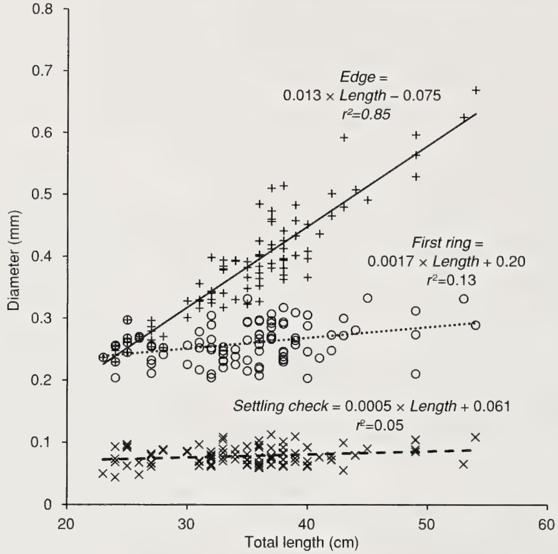

Figure 8

Relationships between the diameters of marks on illicia and total lengths of goosefish (*Lophius americanus*) captured along the Atlantic coast from Virginia to Georges Bank from May 2015 through July 2017. Multiplication signs, circles, and crosses indicate values for diameters of settling checks, first rings, and edges of illicia, respectively. For each type of mark, trend lines, linear regression equations, and coefficients of correlation (r^2) are shown.

low precision of readings of illicia in our study. Other relevant factors may be the age reader's limited experience with the structure and possible differences in lighting between the 2 readings. The age reader did not identify the same rings and may have picked a different position for the first ring each time. However, the reader was careful to avoid counting a false annulus, as is seen in other *Lophius* species. This false annulus was identified in 14 of the 22 images of illicia from goosefish annotated by J. Landa (Landa[5]).

Recommendations for reading illicia of other *Lophius* species (Duarte et al.[1]) include starting with larger (>50 cm TL) fish and adjusting the lighting and focus as each sample is viewed. The fish in this study were mainly smaller than 50 cm TL, precluding the first suggestion, although the samples used by Bank et al. (2020) were mainly over 50 cm TL. The age reader in our study adjusted the microscope while viewing samples; however, it was impossible to do so during training on images.

The age reader's vertebral ring counts never agreed with known ages and were always higher than the known age (often by 2–3 years). Overestimation of ages derived from vertebrae also occurred for the 2 smallest fish in the study by Bank et al. (2020). Possible reasons for the overestimation of vertebral ages include checks due to sporadic feeding behavior, variation in short-term growth rates, and variation in temperature as the fish migrate vertically (Bank et al., 2020). In our study, precision of vertebral ring counts was below acceptable levels but was much higher than ring counts from illicia. The differing levels of precision may have been because of the age reader's greater level of experience with vertebrae than with illicia or because of the false annuli and multiple checks seen in illicia.

Marginal increment analysis

Results from marginal increment analysis (Fig. 7) provide evidence of annual formation of rings on the illicium. However, the analysis was not conclusive as a result of low sample sizes, high variability, and a short time span (13 months). This analysis included only fish of ages from 1+ to 2+ years; therefore, these results should not be applied to older age classes.

We followed Campana's (2001) guidelines for implementing marginal increment analysis as much as was feasible: we made an effort to view samples in random order and examined only one year class. Our sampling did not extend for 2 years, as recommended, and use of larger sample sizes may have revealed a cyclic pattern. However, our results provide a provisional estimate of the timing of ring formation.

Growth

Growth rates estimated from modal length progression of the 2015 year class (11–16 cm TL/year; Table 1) were much faster than estimates based on readings of vertebrae or illicia in our study (Fig. 9). Our illicium-derived growth estimates (7–10 cm TL/year) were slightly faster than our vertebra-derived estimates (5–10 cm TL/year). The vertebral estimates were similar to those from earlier studies in which vertebrae were used (6–10 cm TL/year; Richards et al., 2008), indicating that the aging method was applied similarly in the 2 time frames and that the 2015 year class grew normally.

Our estimate of growth in the first few months of life (1.52 mm/d) is comparable to the rates of 1.4 mm/d (pelagic) and 1.3 mm/d (benthic) for young-of-the-year fish found by Able et al. (2007), who had a larger sample size (n=60) than that of our study. However, our observations of

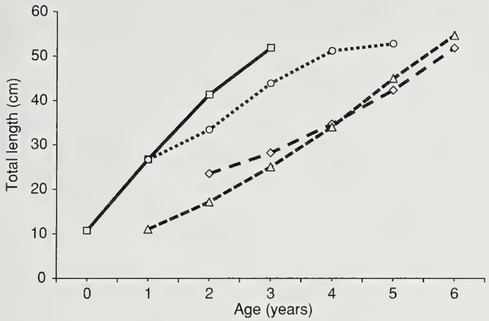

Figure 9

Mean lengths at age of goosefish (*Lophius americanus*) captured in the spring along the Atlantic coast from Virginia to Georges Bank, as estimated from 4 sources: modal analysis of length frequencies of fish from the 2015 year class caught in surveys during 2015–2018 (squares), readings of illicia from fish captured for this study (circles), readings of vertebrae from fish captured for this study (diamonds), and readings of vertebrae from historical data in Richards et al. (2008) (triangles).

young-of-the-year fish attaining lengths of 10 cm TL shortly after settlement conflict with the conclusion by Able et al. (2007) that the first annulus is laid down at an average length of 9.6 cm TL. A settlement check or false annulus may have been misinterpreted as an annulus in the Able et al. (2007) study.

In a number of *Lophius* species, growth curves derived from age estimates from vertebrae, illicia, or otoliths have been approximately linear with little evidence of slowing with age (Fariña et al., 2008; Maguire et al., 2008). However, past results for white anglerfish indicate that too many rings may be counted and that growth may be underestimated, particularly among young fish (≤3 years) (Velasco et al., 2008). Our results indicate a similar pattern of underestimation of size at age up through age 3 in goosefish. Faster growth at earlier ages would be expected to result in a curvilinear growth curve, as is typical of most fish species, even if size at age for older fish was essentially linear.

Our revised understanding of the growth of goosefish in the first few years of life brings it more in line with knowledge of the growth of a congener in Europe, the white anglerfish, which reaches about 40 cm TL by age 2 (Jónsson[7]). This size closely matches the 42 cm TL modal length we observed in our study for goosefish at age 2 (in June 2017). Maximum observed size is comparable between the 2 species, given that the maximum observed size is 138 cm TL for goosefish (Richards et al., 2008) and 125–142 cm for white anglerfish (Jónsson[7]; Landa et al., 2013; Ofstad et al., 2013).

The observed growth rate, based on the progression of the length mode for goosefish at ages 0–3, is faster than previously thought. This finding has implications for our understanding of productivity in this species. Previous measurements of the length at which 50% of fish reach sexual maturity are 38 cm TL in males and 44 cm TL in females (Richards et al., 2008). Age estimates associated with these lengths are 4.3 years for males and 4.9 years for females (Richards et al., 2008). Results of our study indicate that goosefish instead reach the median length at maturity in their first 2 years. Similarly, the minimum legal size in the fishery (43 cm TL), previously thought to correspond to ages 4–5 (Richards et al., 2008), would instead correspond to age 2 under our current understanding. More research, and an effective method for estimating ages, will be needed to develop a full growth curve.

Conclusions

Results of our validation study indicate that ages cannot be estimated from either illicia or vertebrae of goosefish at present. Although results of the marginal increment analysis indicate that a ring is laid down on the illicium in spring–summer, age estimates from both illicia and vertebrae had insufficient levels of accuracy and precision to be used for age estimation.

Despite this outcome, important observations were made about growth rates in goosefish. Size at age 3 was nearly double previous estimates from vertebral aging, indicating that the species has higher productivity than has previously been thought.

It remains important to find a valid aging method for this species so that growth rates can be modeled and the population can be managed more effectively. Other structures, such as the operculum or other bones (Elzey et al., 2015), may be worth investigating. Other future efforts could include microchemical analysis (Siskey et al., 2016) or staining (Natanson et al., 2007), which could help in identifying annuli in illicia or vertebrae. In-person training to learn methods for reading illicia from experienced personnel in Europe may also help with reading illicia of goosefish.

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Reproductive characteristics for the blue shark (*Prionace glauca*) in the North Atlantic Ocean

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Abstract—The blue shark (*Prionace glauca*) in the North Atlantic Ocean is caught in large numbers in commercial fisheries and faces the possibility of overfishing. Reproductive parameters, such as size and age at maturity, are important descriptors of life history characteristics used for understanding and managing marine organisms but have not been evaluated for the western North Atlantic Ocean since 1979. To address this gap in knowledge, we used samples from 369 female and 488 male blue sharks collected during 1971–2016 and examined whether maturity parameters have changed over time. We compared sex-specific fork length (FL) (L_{50}) and weight (W_{50}) at median maturity between 2 time periods (1971–1977 and 2003–2016). No evidence of change in either L_{50} or W_{50} was observed for females. Males had a statistically significant increase in both parameters; however, this increase was likely the result of differences in sample size range between the time periods. Thus, all data from 1971 through 2016 were combined to obtain new estimates of age and size at 50% maturity for both sexes. The L_{50} and W_{50} are 192.5 cm FL and 49.5 kg for male blue sharks and 190.9 cm FL and 50.1 kg for female blue sharks. These updated L_{50} and W_{50} increase reliability of data inputs for fisheries management.

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The blue shark (*Prionace glauca*) is a pelagic species with a circumglobal distribution in tropical, subtropical, and warm temperate seas, including the Mediterranean Sea (Compagno, 1984). This species has long been considered the most abundant of the Atlantic pelagic sharks (Bigelow and Schroeder, 1948), ranging from Newfoundland, Canada, to Argentina in the west, from Norway to South Africa in the east (Bigelow and Schroder, 1948; Castro, 2011), and over the entire mid-Atlantic (Aasen, 1966). Evidence from tagging data indicates that North Atlantic blue sharks constitute a single stock with seasonal latitudinal migrations (Kohler et al., 2002; Kohler and Turner, 2019). Additionally, results from genetic studies indicate not only a single North Atlantic population but a single global blue shark population (Veríssimo et al., 2017). However, differences do exist in various geographic areas in maximum and average size and in size and age at maturity (Skomal and Natanson, 2003; Mejuto and García-Cortés, 2005), making regional studies on life history important for local management.

Different stages of the blue shark reproductive cycle are believed to occur in different areas of the North Atlantic Ocean (Pratt, 1979). The blue shark is a placental viviparous species, with broods usually ranging from 25 to 50 young born after a gestation period of 9–12 months (Pratt, 1979), and Aasen (1966) suggested an average brood size of 45 young in the same area. Brood size in the blue shark appears to be regionally variable (Mejuto and García-Cortés, 2005; Castro, 2011) with up to 135 young reported from a brood in the Indian Ocean (Gubanov and Grigor'yev, 1975) and averages varying from 25.6 young in the North Pacific Ocean (Nakano, 1994) to 37 young in the Gulf of Guinea (Castro and Mejuto, 1995). Brood size has also been shown to increase with female size (Mejuto and García-Cortés, 2005). Although few gravid females in the western North Atlantic Ocean have been reported (Pratt, 1979), many have been caught off the coast of Africa, the Madeira Islands, and the Canary Islands (Aasen, 1966; Mejuto and García-Cortés, 2005; Kohler and Turner, 2008), indicating the possibility of offshore parturition grounds. Pratt (1979) suggested that parturition occurs between March and July in the eastern North Atlantic Ocean but noted that young-of-the-year (YOY) individuals are infrequently encountered in coastal waters. In the central North Atlantic Ocean, the presence of mature females in advanced stages of pregnancy during spring and the appearance of the smallest size classes of YOY in early summer indicate that the archipelago of the Azores is a parturition area (Aasen, 1966; Vandeperre et al., 2014). Additionally, the occurrence of neonate- and YOY-sized sharks on the Grand Banks of Newfoundland, a widely used fishing ground off Newfoundland, indicates that this area may also be a parturition or nursery area for the blue shark (L. Natanson, unpubl. data).

Blue sharks represent the most frequently captured shark in the U.S. Atlantic pelagic longline fishery, with high catch rates in the Grand Banks of Newfoundland (Mandelman et al., 2008). Throughout the world's oceans, blue sharks are taken by using diverse fishing gear, but they are caught mostly as bycatch on pelagic longlines targeting tuna and billfish (Bonfil, 1994; Mandelman et al., 2008). Additionally, as other stocks of large pelagic fish species declined, several nations bordering the North Atlantic Ocean specifically targeted blue sharks for their fins and meat (Castro et al., 1999; Mejuto et al., 2002).

Data reported by the International Commission for the Conservation of Atlantic Tunas (ICCAT) indicate that the overall catch of blue sharks in the North Atlantic Ocean increased between 1993 and 2016 (from 9589 metric tons [t] to 44,067 t), followed by a decrease between 2016 and 2017 (from 44,067 t to 39,675 t) (ICCAT[1]). The North Atlantic blue shark population is not considered overfished at this time (ICCAT[1]); however, there is uncertainty in data inputs, such as size, and there were problems with the production models fitting the data, leading to uncertainty in the results. Therefore, the possibility of the stock being overfished or subjected to overfishing cannot be ruled out (ICCAT[1]). Recognizing this uncertainty, and that blue sharks are caught in large numbers, the ICCAT recently implemented an annual total allowable catch of 39,100 t for the conservation of blue sharks in the Atlantic Ocean (ICCAT[2]).

As fisheries managers set policy guidelines on the basis of the results of stock assessment models that rely on life history data (Hilborn and Walters, 1992), there is a need to understand and periodically reevaluate the life history of a species. Reproductive potential is a vital component of life history data; however, maturity data on highly migratory pelagic sharks, such as the blue shark, are often lacking (Cortés, 1998; Castro, 2011). Pratt (1979) is the most recent publication specifying sizes at maturity for blue sharks in the western North Atlantic Ocean. Since those data were collected, changes have occurred in fishing pressure, which has been suggested to have the potential to affect the blue shark population (ICCAT[1]), and climate change could also alter the biology of species because of changes in prey that lead to shifts in growth (Pinsky et al., 2019). Thus, the objectives of this study were 1) to provide current estimates of size at maturity for blue sharks, including length and weight at median maturity (L_{50} and W_{50}, respectively) for both sexes, and 2) to determine if changes in reproductive characteristics have occurred over time in the blue shark.

Materials and methods

Specimen collection

Specimens of blue sharks were collected opportunistically between 1971 and 2016 from commercial and recreational fishermen, at shark tournaments, and during National Marine Fisheries Service research surveys along the northeastern coast of North America, between New Jersey and the Flemish Cap. A subset of the maturity data analyzed (number of samples [n]=338) was previously used to estimate maturity parameters by Pratt (1979). For most specimens, full dissections were completed by experienced personnel using consistent protocols. Because of time constraints during shark tournaments, it was not always possible to complete a full dissection on each specimen. When time was limited, an assignment of maturity was made through visual examination of organ condition on the basis of the dissectors' experience of organ maturity from previous detailed dissections.

Morphometrics

Fork length (FL) was measured in centimeters on each specimen following Kohler et al. (1995; from the tip of the snout to the fork of the tail, over the curvature of the body). Individuals were weighed (in pounds or kilograms) when possible; all weights were converted to kilograms. To allow direct comparison to data from this study, median total lengths (TLs) at maturity presented in other studies (Megalofonou et al., 2009; Carrera-Fernández et al., 2010; Bustamante and Bennett, 2013; Jolly et al., 2013) were converted to FL by using the following equation from Kohler et al. (1995):

$$FL = 0.8313(TL) + 1.3908 \quad (n=572, r^2=0.99). \qquad (1)$$

Maturity

Maturity condition was determined by measurements and visual examinations noting condition and appearance of external and internal reproductive organs following Pratt (1979). Reproductive terminology follows Pratt (1979), Hamlett (1999), and Hamlett and Koob (1999). Only the right ovary in the blue shark is functional (Pratt, 1979); thus, for all specimens, reproductive organs from the right side of the body were measured to the nearest millimeter to ensure consistency. Each fish was examined fresh to assign a mature or immature (juvenile) status, and detailed conditions, such as foreign objects in the body or excessive thinness, etc., were noted. Mature females were further classified as gravid or postpartum when appropriate. Gravid females contained embryos, and postpartum females had evidence of recent past pregnancy, such as flaccid uteri or ovaries in the process of oogenesis. Juveniles with lengths between the smallest mature and largest immature sizes (transitional range) were further examined given that these sizes were in the range of median size at maturity, and because of the gradual nature of maturation, it was difficult to ascertain their condition.

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[1] ICCAT (International Commission for the Conservation of Atlantic Tunas). 2018. Report of the Standing Committee on Research and Statistics (SCRS) (Madrid, Spain, 1 to 5 October 2018), 298 p. ICCAT, Madrid, Spain. [Available from website.]

[2] ICCAT (International Commission for the Conservation of Atlantic Tunas). 2019. Recommendation by ICCAT amending the recommendation 16-12 on management measures for the conservation of the North Atlantic blue shark caught in association with ICCAT fisheries. ICCAT Rec. 16-12, 2 p. [Available from website.]

Female blue sharks were visually examined for the presence or absence of mating scars or injuries. Internal measurements included the width (measured at the widest point) of the upper oviduct and oviducal gland, uterus width and length, and ovary width and length. The diameter of the largest oocyte was measured, and the presence or absence of the vaginal membrane (hymen) was determined by insertion of a probe through the posterior end of the uterus into the cloaca; the latter was used as an indicator of prior mating activity.

For males, maturity was externally assessed by examination of clasper condition on the basis of degree of clasper calcification (fully calcified, partially calcified, or uncalcified), ability of the clasper to easily rotate around the base, and the ability of the rhipidion to open (Clark and von Schmidt, 1965). Clasper length was measured on the external side from the insertion of the pelvic fin to the tip of the clasper. Siphon sacs, which lie between the skin and the abdominal musculature, were measured as per Natanson and Gervelis (2013). Internal measurements for males included epididymis width, ampulla epididymis width, and testis length and width. Presence or absence of spermatophores was noted, as was coiling of the epididymis.

For sharks that did not undergo a full workup, maturity was assessed on the basis of visual examination following criteria from Pratt (1979). In females, the condition of the epigonal tissue encasing the ovaries, presence and size of oocytes, and the general appearance of the upper oviduct, oviducal gland, and uterus were examined. In males, the clasper condition (as described in the previous paragraph), the amount of the epigonal tissue surrounding the testis, and coiling of the epididymis were examined. The specimens were then classified on the basis of development of these characteristics.

Measurements of the reproductive organs of both sexes were plotted against FL to examine the growth of the organs throughout ontogeny. Those specimens not assigned a maturity status at the time of dissection were later classified on the basis of comparisons of organ measurements in relation to FL, comparisons with organ measurements of staged individuals, and detailed notes on condition taken at dissection. Non-staged specimens within the transitional size range could not be assigned a status by using measurements alone because of the overlap of immature and mature stages in this size range. For some samples, there was not enough information to confirm maturity stage; thus, none of these samples were used in the ogive analyses.

Pratt (1979) assigned 3 maturity stages for female blue sharks: immature (46.0–145.0 cm FL), subadult (145.0–185.0 cm FL), and mature (185.0–300.0 cm FL). In the subadult phase, the organs necessary for copulation were developed, while those required for generation (such as oviducal gland and ovaries) were still developing. Therefore, for ogive analysis in our study, we considered immature any samples that would be assigned to the subadult stage in his classification.

Median maturity analysis

Median FL and weight at maturity were calculated for both sexes by using maturity ogives fit to binomial data on reproductive maturity status. The probability that a given individual i was mature was modeled as the outcome of a Bernoulli random variable, where y_i is 0 for immature individuals and is 1 for mature individuals:

$$y_i \sim \text{Bernoulli}(p_i), \tag{2}$$

where p_i = the probability that shark i is mature.

To examine life history changes through time, samples were divided into 2 discrete time periods (TPs). Time period 1 (TP1) corresponded to the data collected during 1971–1977, data that were originally analyzed by Pratt (1979). Time period 2 (TP2) included specimens collected during 2003–2016, primarily by L. Natanson. The gap between time periods is approximately 5 generations, allowing time for density-dependent changes in life history.

We modeled p_i as a function of size (separately in terms of FL and weight) and time period as follows, with the logit link function constraining p_i to values between 0 and 1:

$$\text{logit}(p_i) = \beta_0 + \beta_{1,\text{Period}}\, Size_i, \tag{3}$$

where β_0 = an intercept term representing the mean probability that a shark is mature; and

β_1 = the time-period-specific effect of size in terms of either FL or weight.

Models were fit to data on each sex separately by using maximum likelihood methods with functions available in R, vers. 3.6.3 (R Core Team, 2017). Models were run separately by sex because it is well-documented that life history characteristics (e.g., size at maturity) differ between male and female elasmobranchs (Cortés, 2000). Model fit was evaluated by using the Akaike information criterion corrected for small sample sizes (AIC_c) (Akaike, 1973; Burnham and Anderson, 2002). The best fitting model was the model with the lowest AIC_c value. The difference in AIC_c between each model (Δ_i) was calculated as $\Delta_i = AIC_{c,i} - AIC_{c,\min}$, where $AIC_{c,i}$ is the AIC_c for time period i and $AIC_{c,\min}$ is the lowest AIC_c

for the best fitting model (Burnham and Anderson, 2002). Models with Δ_i values ≤2 are indicative of no evidence of a statistical difference between models. Those with Δ_i values >10 are indicative of poor fit relative to the best fitting model and are generally unsupported.

On the basis of the selected model, the median size at maturity (i.e., L_{50} or W_{50}, the inflection point of the relationship where P=0.5) was calculated from the fitted model parameters as $-\beta_0/\beta_1$. Confidence intervals around L_{50} and W_{50} were bootstrapped from the selected model to 1000 repeated samplings of the maturity data (Harry et al., 2013) by using the boot package (vers. 1.3-20; Canty and Ripley, 2017) in R. For all models, normalized diagnostic plots of the residuals were examined visually to evaluate the appropriateness of model assumptions (Zuur et al., 2010).

Revisiting Pratt (1979)

Pratt (1979) did not present a value for median size at maturity for females. Using Pratt's data (TP1) and staging the subadult phase as immature, we calculated median size at maturity for females. Additionally, for comparison to his analysis, we calculated the male median sizes at maturity using the TP1 data.

Median age at maturity

To improve existing age-structured relationships, age at median maturity was estimated by inserting the calculated L_{50} for each sex into the sex-specific von Bertalanffy growth functions calculated by Skomal and Natanson (2003).

Results

Specimen collection

A total of 857 blue sharks were dissected for reproductive analysis (488 males and 369 females) between 1971 and 2016. Samples were obtained in all months, with most of the samples obtained between June and September (79.3%, n=680) and the remainder between October and May (20.6%, n=177) (Table 1). Recreational fishermen caught the majority of sharks (66.6%, n=571), followed by commercial fishermen (23.3%, n=201), and scientists on research vessels (8.8%, n=75). The source of 1.3% (n=11) of samples could not be determined because the source was not noted at the time of dissection (Suppl. Table 1) (online only). Sharks from the entire study ranged in size between 62.0 and 300.0 cm FL and between 1.0 and 213.4 kg, although size ranges of samples and number of samples were different in each time period and analysis (Table 1).

Maturity

Females Data collected from 1971 through 2016 were used to examine female reproductive condition (see the

Table 1

Number and size range (in centimeters and kilograms) of blue sharks (*Prionace glauca*) by sex, time period (TP), and month of capture per TP in the western North Atlantic Ocean along the northeastern coast of North America between New Jersey and the Flemish Cap. Sampling occurred in 2 TPs: 1971–1977 (TP1) and 2003–2016 (TP2). Values are also provided for the interim period of 1978–2002. n=number of samples.

	Males			Females		
	TP1	1978–2002	TP2	TP1	1978–2002	TP2
n	155	109	224	183	76	110
Fork length (cm)	102.0–279.0	62.0–285.0	64.7–300.0	108.0–263.0	114.0–273.0	63.0–257.0
Weight (kg)	17.7–122.5	1.0–174.0	1.4–213.4	9.1–112.5	8.2–146.0	1.7–110.0
January	0	0	0	0	1	0
February	0	2	0	0	4	0
March	6	2	0	6	2	0
April	1	2	0	1	3	0
May	40	4	0	3	2	0
June	36	35	105	65	38	9
July	56	47	46	53	15	1
August	1	7	21	15	7	10
September	2	2	43	21	0	45
October	13	3	9	19	0	45
November	0	4	0	0	4	0
December	0	1	0	0	0	0

"Median maturity analysis" section). Maturity condition was not defined for 54 specimens, of which 30 specimens were in the transitional size range and thus could not be judged. Data collected on the additional 24 specimens was not sufficient to determine reproductive condition; therefore, these specimens were not assigned a reproductive condition and were not used in ogive analysis. A sharp increase in growth of organ size relative to FL was apparent in all reproductive organs of females (Fig. 1, Suppl. Figs. 1–3 [online only]).

Juvenile females ranged in size between 63.1 and 206.0 cm FL and between 1.7 and 59.0 kg (*n*=238). Juveniles lacked mating scars and possessed a vaginal membrane. Juvenile females possessed a thin oviduct and varying stages of differentiation of the oviducal gland. In the smallest samples, the right oviducal gland was small and barely distinguishable from the oviduct. Additionally, the paired uteri were thin and indistinguishable from the lower portion of the oviduct; as growth progresses these organs enlarge and become more defined. Ovaries in juveniles were enclosed in epigonal tissue, and the smallest individuals had no oocytes visible to the naked eye (Table 2).

Because of the gradual process of maturity, there is a transitional size range between the smallest mature and largest juvenile fish (173.0–206.0 cm FL and 28.1–59.0 kg). In this size range, specimens can be mature or immature. The organs of juveniles can have both mature and immature characteristics because the organs develop at differing rates. Fifty-six juveniles fell within this size range. In general, the ovaries of juveniles in the transitional size range were developing oocytes (4.0–16.0 mm), the oviducal gland was expanding and becoming differentiated from the oviduct (22.0–35.0 mm), and the uterus had begun to thicken (Table 2, Fig. 1, Suppl. Figs. 1–3 [online only]).

Mature females ranged in size between 173.0 and 273.0 cm FL and between 32.7 and 146.0 kg (*n*=77). The uterus of mature females varied in size and elasticity, a flaccid uterus indicated recent or past pregnancy, and gravid females carried embryos (Table 2, Suppl. Fig. 3 [online only]). Mature ovaries ranged from developing new oocytes (~4.0 mm) after recent

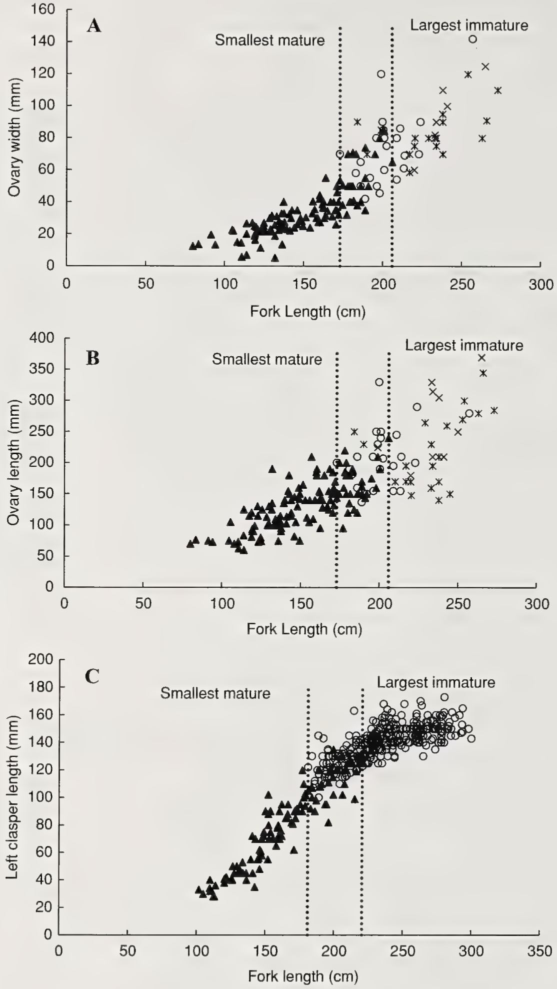

Figure 1

Relationships of (**A**) ovary width (in millimeters) and (**B**) ovary length (in millimeters) to fork length (in centimeters) of female blue sharks (*Prionace glauca*) and of (**C**) left clasper length (in millimeters) to fork length (in centimeters) of male blue sharks caught during 1971–2016 in the western North Atlantic Ocean along the northeastern coast of North America between New Jersey and the Flemish Cap, by maturity stage. Black triangles and open circles indicate specimens of both sexes in the immature and mature stages, respectively. Symbols indicate further classification of mature females as gravid (*) or postpartum (×). The vertical dotted lines represent the lengths of the smallest mature and largest immature samples.

Table 2

Ranges of measurements and descriptions of organs used to determine maturity stages of female blue sharks (*Prionace glauca*) captured in the western North Atlantic Ocean between New Jersey and the Flemish Cap during 1971–2016. Sharks in the size ranges associated with the juvenile and mature stages generally conform to those assignments (unless otherwise noted); whereas, sharks in the transitional size range can be either immature or mature and represent the size of the smallest mature and largest juvenile fish. The table format is adapted from Walker (2005). n=number of samples.

Organ	Range of organ measurement (mm)	Description	Maturity stage
Ovary length (n=183)	≤136	Enclosed in epigonal tissue, clear or no visible oocytes	Immature
	<136 to >240	Thinning epigonal tissue, follicles become opaque	Transitional
	≥240	Little epigonal tissue, oocytes range from new developing to turgid yolked oocytes	Mature
Ovary width (n=159)	≤42	Thin, difficult to distinguish from epigonal tissue	Immature
	<42 to >80	Thinning epigonal tissue, widening with developing oocytes	Transitional
	≥80	Thin epigonal tissue, defined shape, follicles range from new developing to turgid yolked oocytes	Mature
Egg diameter (n=296)	≤4	Clear or non-visible follicles, contained in layer if generative tissue	Immature
	>4 to <16	Follicles become opaque	Transitional
	≥16	Yolked oocytes	Mature
Oviducal gland width (n=273)	≤22	Thin, undifferentiated from the upper oviduct	Immature
	>22 to <35	Begins to take shape, differentiated from the upper oviduct	Transitional
	≥35	Plump, heart shaped	Mature
Uterus width (n=290)	≤14	Thin, undifferentiated from the oviduct	Immature
	>14 to <35	Widens from the oviduct	Transitional
	≥35	Tissue thickens, elastic or flaccid	Mature
Uterus length (n=91)	≤260	Thin, undifferentiated from the oviduct	Immature
	>260 to <540	Differentiated from the oviduct, widening and elongated	Transitional
	≥540	Elongated and flaccid	Mature
Upper oviduct width (n=132)	≤5	Thin tube	Immature
	>5 to <12		Transitional
	≥12	Thickens, differentiated from oviducal gland	Mature

birth to turgid, large oocytes (29.0 mm) that were ready for ovulation (Table 2, Suppl. Fig. 1 [online only]). In mature specimens, the oviduct was fully differentiated from the oviducal gland, which was plump, heart shaped, and ≥35 mm in width. The status of mature females was further staged as gravid (n=32) and postpartum (n=11).

Males Data collected from 1971 through 2016 were examined to determine male reproductive condition (see the "Median maturity analysis" section). Sharp increases in organ size relative to FL for clasper length, testis length, and epididymis width indicate that they are good indicators of L_{50} (Fig. 1, Suppl. Fig. 4 [online only]). In contrast, the siphon sac length, ampulla epididymis width, and testis width had slower gradual growth when plotted against FL and are not adequate indicators of L_{50}.

Immature males (n=148) ranged between 64.7 and 220.5 cm FL and between 1.4 and 68.5 kg, and they were characterized externally by soft, uncalcified, or partially calcified claspers that resisted rotation and opening of the tip (Table 3). The siphon sacs of juvenile males were constricted and did not extend fully to the pectoral girdle. In this stage, the epididymis was thin and straight, and the testes were entirely encompassed in epigonal tissue. In some juvenile males, sperm was present.

Immature males in the transitional size range were maturing, and their organs often had both mature and immature characteristics. Although most fish in this size range were staged as mature or immature, data collected on 5 specimens (180.5–191.2 cm FL) did not provide enough information to determine reproductive condition; therefore, these specimens were not assigned a condition and were not used in ogive analysis. Immature sharks in the transitional range were found to have testes enclosed in thinning epigonal tissue, a coiled epididymis, and flexible claspers. In 5 cases, males with mature internal organs had partially calcified claspers. These individuals ranged in size between 188.5 and 228.0 cm FL, overlapping the transitional size range that may indicate that clasper calcification is the best indicator of maturity.

Mature males ranged between 181.0 and 300.0 cm FL and between 35.4 and 213.4 kg (n=331). Claspers of mature males (>220.5 cm FL) were elongated (≥123 mm; Fig. 1), fully calcified, easily rotated, and opened at the tip. A mature epididymis was heavily coiled, and the mature testis was surrounded by a thin layer of epigonal tissue

Table 3

Ranges of measurements and descriptions of organs used to determine maturity stages of male blue sharks (*Prionace glauca*) captured in the western North Atlantic Ocean between New Jersey and the Flemish Cap during 1971–2016. Sharks in the size ranges associated with the immature and mature stages generally conform to those assignments (unless otherwise noted); whereas, sharks in the transitional size range can be either immature or mature and represent the size of the smallest mature and largest immature fish. The table format is adapted from Walker (2005). *n*=number of samples.

Organ	Range of measurement (mm)	Description	Maturity stage
Left clasper length	≤99	Soft and uncalcified, resists rotation and flexing of the tip	Immature
(*n*=434)	>99 to <135	Soft or plastic, begins to rotate	Transitional
	≥135	Calcified, easy rotation and flexing of the tip	Mature
Epididymis width	≤13	Thin and straight	Immature
(*n*=330)	>13 to <23	Coiling begins	Transitional
	≤23	Thickened and heavily coiled	Mature
Testis length	≤105	Thin, encompassed in epigonal tissue	Immature
(*n*=322)	>105 to 190	Thinning epigonal tissue, elongated	Transitional
	≥190	Elongated, distended	Mature

(Table 3). Sperm and spermatophores were observed in all mature males for which this factor was examined.

Median maturity analysis

Females Variation in size at maturity for females was best described by maturity ogives based only on FL or weight, indicating no evidence of difference in L_{50} or W_{50} between time periods (Table 4, Suppl. Table 2 [online only]); therefore, all data from 1971 through 2016 were used to define the size at median maturity. On the basis of maturity ogives, the size at median maturity of female blue sharks is 190.9 cm FL and 50.1 kg (Table 4, Fig. 2).

Males Contrary to the results for females, results from the best fitting model for males indicate an increase in L_{50} and W_{50} between time periods (Table 4, Suppl. Table 2 [online only]). Estimated median maturity for TP2 occurred at 211.2 cm FL and 62.3 kg, which represent rather large increases from TP1 (184 cm FL and 35.6 kg). Upon further examination, there appeared to be clear differences in the sampled size distribution between time periods, with TP2 having more large fish (>220 cm FL) and fewer samples in the range of 160–220 cm FL than TP1 (Table 4, Fig. 3). The absence of juvenile males in the range of 220–240 cm FL during TP1, and the presence of juvenile males in the range of 220–240 cm FL during TP2, may indicate an increase in size at maturity over time. However, there is evidence of large juveniles in the interim period (1978–2002), and this evidence indicates that large juveniles were in this size range prior to TP2 and were probably under-sampled because of low sample size in this size range in TP1. Because the large juvenile males were present, the difference observed between TP1 and TP2 is

Table 4

Median fork length (FL in centimeters) and weight (in kilograms) at maturity (L_{50} and W_{50}, respectively) and size range (in centimeters and kilograms) of blue sharks (*Prionace glauca*) captured in the western North Atlantic Ocean between New Jersey and the Flemish Cap. Sampling occurred in 2 time periods: 1971–1977 (TP1) and 2003–2016 (TP2). Values are also provided for the interim period of 1978–2002. *n*=number of samples.

	Size range (cm FL)				L_{50}		Size range (kg)				W_{50}	
Period	Female	*n*	Male	*n*	Female	Male	Female	*n*	Male	*n*	Female	Male
TP1	108.0–263.0	134	102.0–279.0	155	190.6	184.1	9.1–112.5	80	17.7–122.5	33	50.8	35.6
TP2	114.0–273.0	110	64.7–300.0	224	189.8	211.2	1.7–110.0	56	1.4–213.4	199	43.5	62.3
TP1 and TP2	63.1–257.2	244	64.7–300.0	379	189.8	191.2	1.7–112.5	136	1.4–213.4	232	48.3	50.7
1971–2016	63.1–273.0	315	62.0–300.0	488	190.9	192.5	1.7–146.0	188	1.0–213.4	319	50.1	49.5

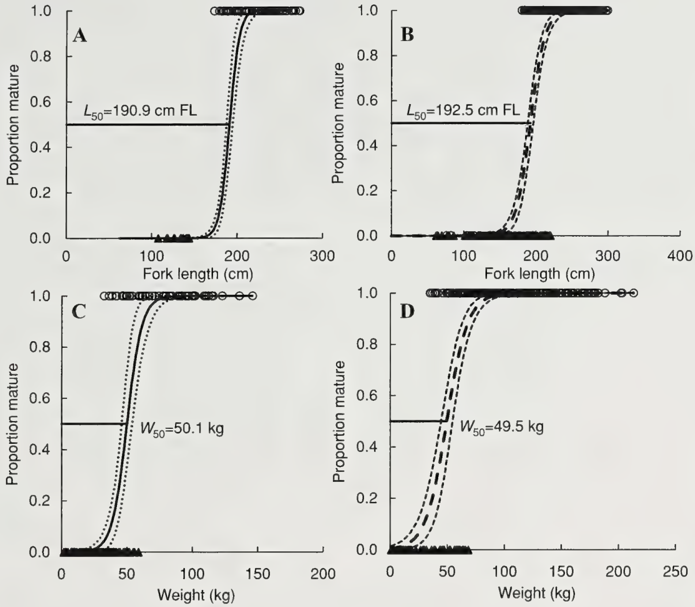

Figure 2

Maturity ogives by sex for blue sharks (*Prionace glauca*) caught in the western North Atlantic Ocean between New Jersey and the Flemish Cap during 1971–2016: fork length (FL in centimeters) for (**A**) females and (**B**) males and weight (in kilograms) for (**C**) females and (**D**) males. Open circles and black triangles indicate individuals in the mature and juvenile stages, respectively. In each panel, a horizontal line indicates and a value is provided for the median length or weight at 50% maturity (L_{50} or W_{50}). The dotted and dashed lines indicate 95% confidence intervals.

likely the result of sampling bias rather than a biologically significant difference. We therefore combined the data for all time periods to provide an updated size at median maturity for males of 192.5 cm FL and 49.5 kg and feel this estimate of current reproductive parameters for the population is robust (Fig. 2).

Revisiting Pratt (1979)

For male blue sharks, we used Pratt's (1979) original staging and found that his estimate of average size at maturity of 183.0 cm FL is lower than our calculated estimate of median maturity (184.1 cm FL) for TP1. We analyzed the female data from Pratt (1979), producing an L_{50} of 190.6 cm FL, which is slightly higher than Pratt's estimated size at first maturity of 185.0 cm FL. Pratt (1979) did not calculate median size at maturity for females; therefore, L_{50} values calculated from his data for TP1 were used for comparison.

Median age at maturity

When the median L_{50} for each sex was combined with the published growth curves from Skomal and Natanson (2003), age at median maturity stayed stable at 5 years for both sexes.

Discussion

Changes in life history characteristics in response to environmental conditions or fishing pressure over time are a concern, particularly with climate change. Additionally, having up-to-date sex-specific inputs is important for management. Results from the statistical comparisons between current and past reproductive characteristics in this study indicate a difference in the parameter estimates for male blue sharks while estimates for females have remained unchanged since the 1970s. For females, L_{50}

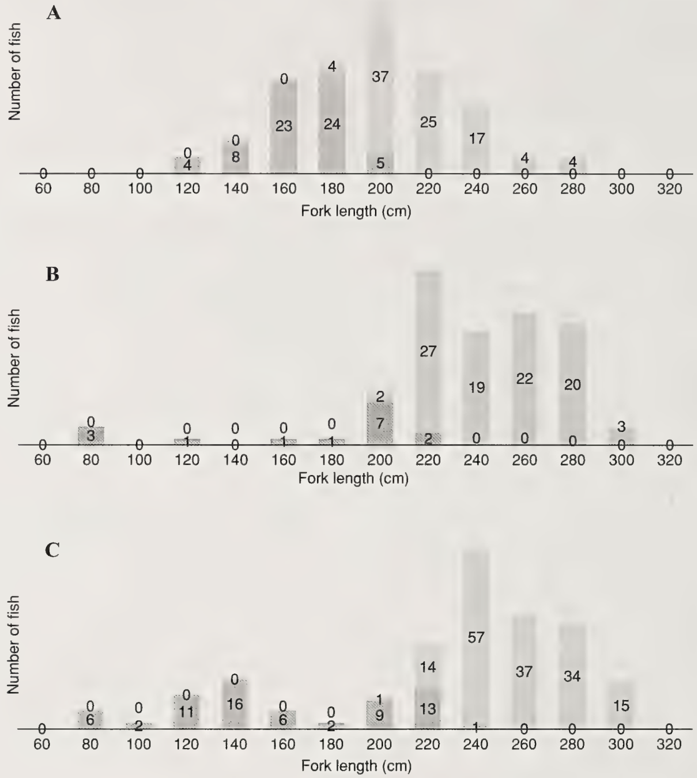

Figure 3

Stacked histograms of length and maturity stage, by time period, for male blue sharks (*Prionace glauca*) caught in the western North Atlantic Ocean: (**A**) time period 1 (1971–1977), (**B**) interim period (1978–2002), and (**C**) time period 2 (2003–2016). Dark gray bars represent values for juvenile fish, and light gray bars indicate values for mature fish. The number of juvenile or mature fish is provided within each bar.

varied slightly, within 10 mm FL for all time periods, and the L_{50} for males increased from Pratt's (1979) estimate (183.0 cm FL original, or 184.1 cm FL recalculated) regardless of what comparison was used (Table 4). However, it is important to determine if this change is real or an artifact of sampling method or sample distribution.

In previous studies on the shortfin mako (*Isurus oxyrinchus*) (Natanson et al., 2020) and the common thresher shark (*Alopias vulpinus*) (Natanson and Gervelis, 2014), comparisons of data over a 40-year period have shown that changes in principal dissectors over time did not affect the data, indicating that, probably because of intensive training and standard protocols, personnel changes were not a factor leading to the maturity shift. However, we had to consider the possibility that changes in maturity analyses or personnel conducting the study may have influenced these results. For example, Pratt (1979) based maturity status on the presence of spermatophores. The current standard for male maturity is clasper calcification (Castro, 2011). Spermatophores have actually been shown to be present before clasper calcification in a variety of species (Castro, 2011), and such presence of spermatophores may have biased the data toward a lower median size at maturity. We restaged data from Pratt (1979) on the basis of clasper calcification and found that his estimate of size at median maturity of 183.0 cm FL is similar to our recalculated estimate of 184.1 cm FL, indicating that our methods for calculating maturity were not the cause of the shift in L_{50} between time periods. Therefore, we conclude on the basis of training and the consistency in results from use of old and new maturity criteria that the differences between time periods are not an artifact of method in dissection, personnel changes, or data analysis.

Another factor that may influence the shift in L_{50} between time periods is sample size distribution and sample availability. The interim period and TP2 both had a larger sample size of bigger sharks than TP1 and, thus, a higher likelihood of larger juvenile specimens, which is what we find in the data (Fig. 3). Because the large (>200 cm FL) juvenile specimens in the interim period were collected close to TP1, it is probable that these specimens were in the western North Atlantic Ocean during TP1, just not sampled, leading to an underestimate of size at maturity in Pratt (1979) and indicating that the real L_{50} was higher at that time and thus no significant change has actually occurred in male characteristics.

We hypothesize that the initiation of shark management led to an increase in large samples in TP2 (Table 4). The increase in sampling of large fish meant that more large juveniles were sampled; large juveniles are proportionally low and were not sampled in TP1 because of a lower overall number of large sharks. Fishing pressure and fisheries management have changed dramatically since the study of Pratt (1979) and were hypothesized to have influenced blue shark sample distribution between TP1 and TP2. Shark management did not start in earnest until the interim period between TP1 and TP2 of this study, meaning that data collection in TP1 was fairly unrestricted and varying size ranges were available. The majority of sampling in all years was conducted at recreational shark tournaments along the East Coast of the United States (Suppl. Table 1) (online only). Early in these tournaments there were no federal, state, or in most cases even tournament catch restrictions of size or number (Castro, 2011). It was not until 1993, when the National Marine Fisheries Service implemented the fishery management plan for sharks of the Atlantic Ocean (NMFS, 1993), that tournament and recreational bag and size limits were imposed (NMFS, 2006). Although some tournaments always had size minima, more of them began to implement size restrictions that were often far higher than those of the federal regulations once management was in place (L. Natanson, unpubl. data). Together, the restrictions of tournaments and federal regulations led to greater sampling of larger sharks. Because the majority of the sampling came from recreational fishermen at tournaments, the sample distribution became skewed to large fish (Fig. 3). Additionally, this influx of large fish led to the increased likelihood of observing large juvenile fish, which are proportionally rarer than the mature fish of that size. The presence of large juveniles would influence the results of the ogive analysis, leading to a higher L_{50}, as we have observed in this study.

Typically, female elasmobranchs reach a larger size than males, presumably because of the need to accommodate gestation (Cortés, 2000). However, in global studies on the blue shark, males have been observed to be larger than females (McKenzie and Tibbo, 1964; Aasen, 1966; Skomal and Natanson, 2003). Similar to our results, median size at maturity of males was found to be greater than that of females in South Africa (Jolly et al., 2013). The L_{50} from our study is greater than those found in other studies of blue sharks globally (Table 5). Pratt (1979) and Hazin and Lessa (2005) reported that both sexes reached first maturity at 5 years; whereas, we found 50% maturity at 5 years, indicating a lower age at maturity for this region. Jolly et al. (2013) reported on differences in age at maturity between the sexes, with males maturing at 7 years as opposed to females maturing at 6 years, again indicating regional differences in life history characteristics despite genetic similarity of this species globally (Veríssimo et al., 2017).

Differences in growth rates between populations of the same species of sharks have been well-documented and found to occur both regionally (e.g., the blacknose shark,

Table 5

Comparison of lengths at median maturity (L_{50}) of blue sharks (*Prionace glauca*) from various life history studies. Measurements of L_{50} have been converted to fork length (FL) by using the relationships from Kohler et al. (1996). The estimated L_{50} of blue sharks in this study represents data collected between 1971 and 2016. NA=not available because a length for females was not reported in the source.

		Length (cm FL)	
Region	Source	Female	Male
Western North Atlantic Ocean	This study	190.9	192.5
Mediterranean Sea	Megalofonou et al. (2009)	179.9	170.1
Baja California Sur, Mexico	Carrera-Fernández et al. (2010)	164.3	154.4
South-east Pacific Ocean	Bustamante and Bennett (2013)	167.0	159.6
South Africa	Jolly et al. (2013)	163.0	168.8
New Zealand	Francis and Maolagáin (2016)	NA	179.4

Carcharhinus acronotus, in the Gulf of Mexico versus the western North Atlantic Ocean; Driggers et al., 2004) and over ocean basins (e.g., porbeagle, *Lamna nasus*; Natanson et al., 2002; Francis et al., 2008). Different environmental conditions can affect growth and other biological processes of marine apex predators (Izzo and Gillanders, 2020). Blue sharks living under different oceanic conditions could have different growth and other life history characteristics (Megalofonou et al., 2009). Thus, it is not surprising that differences exist between oceans in the median size and age at maturity of blue sharks.

The ability to compensate for fishing-induced changes in life history has important implications for the regulation and sustainability of populations (Johnston and Post, 2009). There is evidence that density-dependent compensation and fisheries-induced selection pressure can influence a population's ability to sustain or recover from fishing mortality (Walker, 1998; Cortés, 2007). In a fished population, one might expect an increase in growth rate or a decrease in size at maturity to compensate for higher mortality; however, only a few cases of density-dependent compensation have been empirically described for sharks, and for most species they are poorly understood (Cortés, 1998, 1999, 2007; Walker, 1998). Growth rate has been reported to have increased in juvenile sandbar sharks (*C. plumbeus*) (Sminkey and Musick, 1995) and Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) (Carlson and Baremore, 2003), but no effects have been seen in dusky sharks (*C. obscurus*) (Natanson et al., 2014) following fisheries-induced decreases in abundance. The uncertainty of the North Atlantic blue shark stock leads to the possibility of the stock being overfished or of overfishing occurring (ICCAT[2]); therefore, changes in reproductive characteristics were examined. In this study, we did not observe a change in the reproductive characteristics of blue sharks in over 40 years of sampling.

Conclusions

We reexamined the reproductive characteristics of the blue shark in the Atlantic Ocean. Results of our analysis indicate that the median lengths and weights at maturity did not significantly change from those reported by Pratt (1979). We therefore combined all data from 1971 through 2016 to obtain robust parameter estimates for management. Additionally, the calculated age at maturity also remained the same at 5 years for both sexes.

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Dietary niche overlap and prey consumption for the Steller sea lion (*Eumetopias jubatus*) and California sea lion (*Zalophus californianus*) in northwest Washington during 2010–2013

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Abstract—The diets of Steller (*Eumetopias jubatus*) and California (*Zalophus californianus*) sea lions in northwest Washington are poorly documented. We hypothesized that these species exploit the same prey in Washington because they are both generalist predators that utilize the same haul-out sites and are similar in behavior and body size. We analyzed 776 samples of scat from Steller sea lions and 263 samples of scat from California sea lions collected throughout each year during 2010–2013. The aim of this analysis was to characterize seasonal and annual diets, estimate biomass of prey consumed, and evaluate dietary niche overlap. Steller and California sea lions ate diverse diets that varied seasonally and annually. Primary prey groups for both sea lion species were Clupeidae, Salmonidae, Sebastidae, Rajidae, Pleuronectiformes, Squalidae, and Merlucciidae. We estimated that Steller sea lions ate 11,327 metric tons (t) (standard deviation [SD] 1600) and that California sea lions ate 9063 t (SD 4098) of prey per year during our study. We found significant dietary niche overlap between California and Steller sea lions that feed in northwest Washington.

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The diets of California (*Zalophus californianus*) and Steller (*Eumetopias jubatus*) sea lions have been studied in much of the California Current Ecosystem, yet notable knowledge gaps exist. Diets of populations of California sea lions have been studied at the Channel Islands (Antonelis et al., 1984; Lowry et al., 1991; Lowry and Carretta, 1999; Orr et al., 2011), the Farallon Islands (Bailey and Ainley, 1981), and Monterey Bay (Weise and Harvey, 2008) in California. However, California sea lions, predominately males (Gearin et al., 2017), are distributed north of California as far as Alaska (Maniscalco et al., 2004). Diets of California sea lions north of California are poorly documented with only 2 peer-reviewed published studies (Everitt et al., 1981; Roffe and Mate, 1984) and 3 reports (Reimer and Brown[1]; Scordino[2]; Trites and Rosen[3]). Likewise, the diet of Steller sea lions has been studied in Oregon and Northern California (Riemer et al., 2011), but in Washington it has been reported only in gray literature (Scordino[2]; Wiles, 2015).

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Better knowledge of the spatial and temporal variability of the diets of California and Steller sea lions is needed.

It is likely that California and Steller sea lions utilize the same marine environment for hunting prey because the sympatric species use the same haul-out sites (Mate, 1975) and because adult male California sea lions are similar in size to adult female Steller sea lions and, therefore, have similar physiological limits to dive performance (Weise et al., 2010). It is noteworthy that, although the abundance of the eastern distinct population segment of Steller sea lions increased at an annual rate of 4.25% for pups and of 3.22% for age-1+ sea lions from 1987 to 2017 (Muto et al., 2020), the growth rate of the population was not uniform across its range. The range of the Steller sea lion has contracted northward since the early 20th century with rookeries abandoned in Southern California and abundance at rookeries in central California declining significantly (Pitcher et al., 2007; NMFS, 2013). One hypothesis is that niche competition with California sea lions, which were increasing in abundance (Laake et al., 2018), caused the range contraction (Mate, 1975; NMFS, 2013). Understanding to what degree the dietary niches of California and Steller sea lions overlap will improve our understanding of the ecology of the 2 species and the potential for competition between them.

In this study, we had 3 objectives to advance our knowledge of the diets of California and Steller sea lions in northwest Washington. First, we characterized the diets of both species, including documenting prey diversity and seasonal and annual variability in diet. Second, we performed calculations to estimate the biomass (in metric tons) of fish and invertebrates consumed per year and season by California and Steller sea lions. Last, we used our diet data to evaluate the hypothesis that these sympatric sea lion species have significant dietary niche overlap.

Materials and methods

Study area

Study activities were conducted in northwest Washington (Fig. 1), which is the northernmost extent of the California Current. Relative to other portions of the northern California Current, the waters of northwest Washington have elevated productivity and enhanced biomass of high trophic levels due to geomorphic features and the confluence of the California Current and the Strait of Juan de Fuca (McFarlane et al., 1997; Marchetti et al., 2004; MacFadyen et al., 2008). Year-round sea lion haul-out sites in the study area include the Tatoosh Island Complex (haul-out sites: Tatoosh Island East, Tatoosh Island Cut, and Duncan Rock), Bodelteh Island Complex (haul-out sites: East Bodelteh Island, West Bodelteh Island, Umatilla Reef, and Guano Rock), Carroll Island, and Sea Lion Rock (Fig. 1). At Carroll Island and Sea Lion Rock, 10–20 Steller sea lion pups were born each year during the study period of 2010–2013; both sites now meet the definition of a rookery (Pitcher et al., 2007) with greater than 50 newborn pups counted annually at Carroll Island since 2015 and Sea Lion Rock since 2019 (senior author, unpubl. data). We also surveyed Waadah Island, which is a seasonal haul-out site primarily utilized in the spring.

Field methods

Haul-out counts Vessel-based surveys were conducted by circling haul-out sites and counting sea lions with 7×50 or 8×40 binoculars. When possible, we conducted land-based surveys of East Bodelteh Island. Sea lions at haul-out sites were counted in sections because of the size of the sites and to minimize disturbance by only circling each site once. For each section, we counted the total number of Steller and California sea lions present, and then we recounted the section for 4 demographic groups of Steller sea lions: pups, juveniles, adult females, and adult males. Pups were identified by their darker brown color, chubbier features, and smaller size and were counted from birth (May–July) through 11 months of age (May) (Pitcher et al., 2001). Juveniles were identified as individuals older and larger than pups that had not developed the secondary sexual characteristics of adult males or the size of adult females and were assumed to be between 1 and roughly 5 years of age. Adult females were identified by size, shape, and presence of a pup or dependent juvenile and by having longer whiskers than juveniles (King et al., 2007; Stricker et al., 2015). Adult males were identified by their overall larger size, coarse fur on chest and neck, and large head and foreflippers.

We used the known age of branded individuals (see Wright et al., 2017) to calibrate our methods for classifying demographic groups. No demographic count was assigned if the sea lions entered the water or were arranged too close together to evaluate body shape. We assumed all California sea lions were adult males even though we did observe at least one female identified by the presence of a newborn pup and many juveniles including one that was identified as a 1 year old from San Miguel Island, California, on the basis of its brand number (see DeLong et al., 2017).

We used the demographic counts to calculate the proportion of age-1+ Steller sea lions observed that were adult male, adult female, and juvenile; pups and sea lions not classified to a demographic group were excluded from this calculation. Olesiuk[4] found no significant difference in the proportion of time that age-1+ sea lions spent hauled out by sex or age, indicating that our demographic counts of age-1+ sea lions that were hauled out are representative of the whole population that utilized haul-out sites in northwest Washington during surveys.

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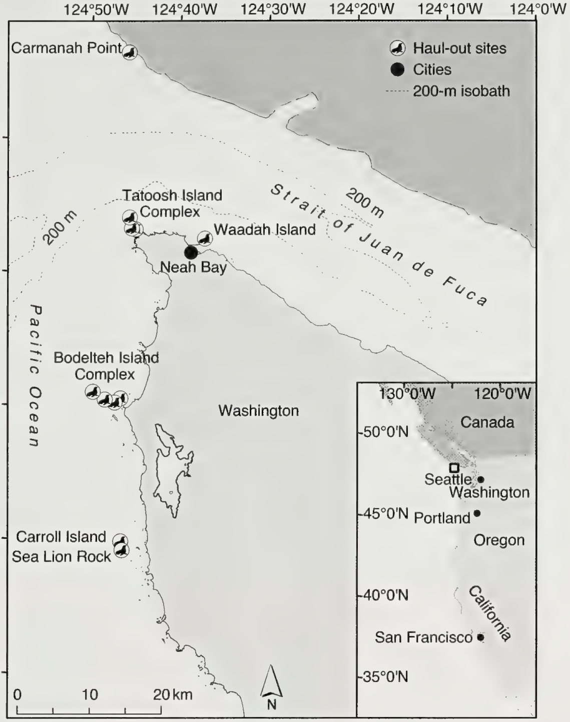

Figure 1

Map of study area of northwest Washington marking haul-out sites of Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) where counts of sea lions and scat collections occurred from 2010 through 2013. The dotted line indicates the 200-m isobath.

Counts of the age-1+ population were included in this analysis only if sea lions at all the haul-out sites in the survey area were counted and, for Steller sea lions, only if a full demographic count was conducted. The exception was that if we had a land-based count for East Bodelteh Island within 10 d of a survey that included all haul-out sites, we used the land-based count for East Bodelteh Island rather than the boat-based count for that day. The counts are minimum estimates of sea lions present because an unknown proportion of the sea lions that were hauled out were not visible during the surveys and, therefore, were not counted (Westlake et al., 1997). We used average counts, rather than maximums, because both species of sea lions are known to change their distribution in response to prey and other factors (Sigler et al., 2009; Womble et al., 2009; Olesiuk[4]; Brown et al., 2020).

Scat collection We collected scat from the Tatoosh Island Complex, Bodelteh Islands Complex, Carroll Island, and Sea Lion Rock (Fig. 1). Locations of scat collections differed by season and were influenced by sea conditions, safety of transferring staff onto the haul-out site, and haul-out utilization by sea lions. Samples of scat of California sea lions were primarily collected at East Bodelteh Island, where large aggregations of California sea lions occur in the spring, early summer, and fall. A central assumption to our sampling method was that scat collected from any haul-out site in northwest Washington was representative of scat of Steller and California sea lions at all haul-out sites in northwest Washington.

Scat samples were collected following procedures described by Lance et al.[5] We were careful to ensure that we collected each scat in its entirety, we avoided collecting scat where multiple scats were likely to be mixed together, and we targeted fresh scat (Akmajian et al., 2017) to minimize potential biases (Staniland, 2002; Bowen and Iverson, 2013). Our goal was to collect 30 scats of Steller sea lions per month and 50 scats of California sea lions per season from August 2010 through February 2013. We defined seasons as follows: December–February as winter, March–May as spring, June–August as summer, and September–November as fall. We targeted haul-out sites, or sections of these locations, where greater than 95% of the sea lions counted at the site were of the species targeted for scat collections. Scats of California sea lions were collected only during the spring, summer, and fall; the difficulty of landing on East Bodelteh Island in winter meant no samples could be collected from the few California sea lions that remained at the site.

Sample processing and prey identification

Scat samples were washed in a residential-style washing machine or through nested sieves by using published procedures (Lance et al.[5]; Orr et al., 2003). Prey hard parts collected from the scat were dried and stored in glass vials. All identifiable hard parts (e.g., bones, otoliths, cartilaginous parts, lenses, teeth, and cephalopod beaks) recovered from scat were examined by using a dissecting microscope and identified to the lowest possible taxon to reduce identification biases (Browne et al., 2002). Prey remains were identified by S. Riemer (of the Oregon Department of Fish and Wildlife, Marine Mammal Program), who used a reference collection of fish and cephalopods from the northeastern Pacific Ocean and coastal estuaries (see Riemer et al., 2011).

Diet analysis

Diet reconstruction We used split-sample frequency of occurrence (SSFO) to reconstruct diets of sea lions because the method produces results that are very similar to volumetric estimates of the composition of prey species in the diets of predators (Olesiuk et al., 1990) because SSFO can be easily incorporated into ecological indices (Krebs, 1999) and because it requires only data on presence and absence of prey (Laake et al., 2002; Tollit et al., 2007). The SSFO approach assumes recovery of remains from all prey consumed and consumption of all prey at an equal volume (Olesiuk et al., 1990). Split-sample frequency of occurrence was calculated by using the following formula:

$$SSFO_{\mathrm{i}} = \frac{\sum_{\mathrm{k}=1}^{\mathrm{i}} \left(O_{\mathrm{ik}} / O_{\mathrm{k}} \right)}{s} \times 100, \tag{1}$$

where $SSFO_{\mathrm{i}}$ = SSFO of taxon i;

O_{ik} = the absence (0) or presence (1) of taxon i in fecal sample k;

O_{k} = the total number of all taxa present in fecal sample k; and

s = the total number of fecal samples that contained identifiable prey.

We present values of frequency of occurrence (FO) in Supplementary Table 1 (online only) to allow comparison to past studies. The following formula was used to calculate FO:

$$FO_{\mathrm{i}} = \frac{\sum_{\mathrm{k}=1}^{\mathrm{s}} O_{\mathrm{ik}}}{s} \times 100, \tag{2}$$

where FO_{i} = the FO of taxon i.

We used 2 definitions of prey taxon. For reporting what prey sea lions ate, prey taxon was defined as the lowest taxon to which a prey item was identified. For calculating ecological indices of diet diversity and dietary niche overlap, we defined prey taxa by prey family, with the exception of flatfish, which were defined by order, and cephalopod and amphibian remains, which were defined by class, because these groups could not be accurately identified to the family level (Sinclair and Zeppelin, 2002). We considered taxa that had an SSFO of 5% or greater to be common prey.

Prey diversity and overlap indices We characterized prey diversity for the 2 sea lion species by using 2 indices: Levin's niche breadth and the Shannon–Wiener diversity index. Levin's niche breadth is sensitive to changes in abundant species, and the Shannon–Wiener index is sensitive to changes in rare species (Krebs, 1999). We used this formula to obtain Levin's niche breadth values (D): $\frac{1}{D}$, where D is $\sum_{\mathrm{i}} p_{\mathrm{i}}^2$ and p_{i} is the SSFO of taxon i. We used this formula to obtain the Shannon–Wiener diversity index values (H):

$$H = -\sum_{\mathrm{i}} (p_{\mathrm{i}} \times \ln(p_{\mathrm{i}})). \tag{3}$$

We used the Morisita–Horn index (Horn, 1966; Krebs, 1999) to compare dietary niche overlap of Steller and California sea lions because it is reported to have the least bias among indices in comparison of diets when prey proportions (like SSFO) are used (Smith and Zaret, 1982). Morisita–Horn index values (MH) were obtained by using the following formula:

$$MH = \frac{2\sum p_{\mathrm{ij}} p_{\mathrm{ik}}}{\sum p_{\mathrm{ij}}^2 + \sum p_{\mathrm{ik}}^2}, \tag{4}$$

where p_{ij} = the SSFO of prey taxon i for population j; and

p_{ik} = the SSFO of prey taxon i for population k.

Dietary niche overlap varies along a scale from 0 to 1, with 1 indicating a complete overlap and 0 indicating no overlap. We considered a value of 0.65 or greater to indicate significant niche overlap (see Aurioles-Gamboa and Camacho-Ríos, 2007; Orr et al., 2011).

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[5] Lance, M. M., A. J. Orr, S. D. Riemer, M. J. Weise, and J. L. Laake. 2001. Pinniped food habits and prey identification techniques protocol. Alaska Fish. Sci. Cent., AFSC Process. Rep. 2001-04, 29 p. [Available from website.]

To accompany the prey diversity and niche overlap indices, we obtained corresponding 95% nonparametric bias-corrected and accelerated bootstrap confidence intervals using 5000 bootstrap samples. The bias-corrected and accelerated bootstrap confidence interval takes into account potential bias and skewness in a bootstrap sampling distribution (DiCiccio and Efron, 1996). The package boot (vers. 1.3-20; Davison and Hinkley, 1997; Canty and Ripley, 2017) was used in statistical software R (vers. 3.6.2; R Core Team, 2019) to calculate each bootstrap sample, bootstrap sampling distribution, and bootstrap confidence interval. Each bootstrap sample was taken with replacement within a given sampling strata.

Prey consumption model

We developed models to estimate average seasonal and annual prey consumption for Steller and California sea lions by using published data sources and data collected during this study for sea lions in northwest Washington for the period from 2010 through 2013.

Simply stated, the model multiplies an estimate of prey consumed per individual per day by the total number of sea lions present in the study area and extrapolates out, by using the number of days in the season, to estimate total prey consumed each season (see Equation 5). We estimated consumption for spring (March–May), summer (June–August), fall (September–November), and winter (December–February) for both California and Steller sea lions. Added together, the seasonal estimates provide a yearly estimate of total consumption for each sea lion species.

To determine annual prey consumption by California and Steller sea lions in northwest Washington during 2010–2013, we used the following equation:

$$\sum_x \sum_y \sum_z (w_{y,z} \times c_{y,z} \times d_x \times n_{x,y} \times p_{x,y,z} \times f_{x,y}) / 1000, \qquad (5)$$

where x = season;

y = the species of sea lion (California or Steller sea lion);

z = the demographic group (adult male, adult female, juvenile male, and juvenile female for Steller sea lions and adult males for California sea lions);

$w_{y,z}$ = the estimated average body weight in kilograms of sea lions of species y and demographic group z.

$c_{y,z}$ = a conditional parameter for the percentage of body weight that the average sea lion of species y and demographic group z eats per day.

d_x = the number of days in season x;

$n_{x,y}$ = the average count of age-1+ sea lions hauled out in the survey area during season x for species y;

$p_{x,y,z}$ = the proportion of sea lions counted in season x, of species y and demographic group z.; and

$f_{x,y}$ = the correction factor for converting the haul-out count to the total abundance of sea lions in the environment of northwest Washington during season x for species y.

California sea lion average body weight was informed by the average body weight of male California sea lions captured at Astoria, Oregon (Wright et al., 2010), and Ballard, Washington (Gearin et al., 2017). The $w_{y,z}$ for Steller sea lions was informed by published body weight estimates for demographic group z (Winship et al., 2001).

The conditional parameter $c_{y,z}$ was informed by published bioenergetics modeling estimates of Winship et al. (2006) for male California sea lions and by demographic group z for Steller sea lions. The bioenergetics models of Winship et al. (2006), the methods of which are described in greater detail in Winship et al. (2002), incorporate energetic costs for lactation and gestation.

The average count of age-1+ sea lions was informed by our surveys as previously described.

We assumed that California sea lions composed a single male demographic group. The $p_{x,y,z}$ for adult female and adult male Steller sea lions were informed directly by the haul-out demographic counts. We were unable to differentiate juvenile Steller sea lions by sex during counts and had to calculate the expected proportion of juveniles that were male or female on the basis of sex-based survival estimates through age 5 for Steller sea lions branded in Northern California and southern Oregon (Wright et al., 2017), assuming an equal sex ratio at birth.

We used a correction factor developed by Lowry and Forney (2005) for counts of California sea lions from aerial surveys at haul-out sites in Northern California. For Steller sea lions, we used the reciprocal of the proportion of age-1+ sea lions hauled out in southern British Columbia (Olesiuk[4]). Olesiuk[4] reported that 36% (coefficient of variation [CV]=2.1%) of age-1+ sea lions were hauled out in winter during the time frame of 1000–1800, when our surveys were typically conducted, and they reported that 67.4% (CV=5.6%) of age-1+ sea lions were hauled out in summer. We applied the winter correction factor for Steller sea lions to the spring and fall because Olesiuk[4] found no significant difference in the proportion of time that satellite-tagged sea lions hauled out in the spring and winter and because Whitlock et al. (2020) found much lower haul-out attendance in the spring than in the summer. The correction factors calculated from data presented by Olesiuk[4] fall within the range and seasonality of the proportion of sea lions observed hauled out by Whitlock et al. (2020). No correction factors were applied for sea lions missed by vessel- or land-based surveys that would have been visible and counted during aerial surveys (Westlake et al., 1997) because no correction values were available in the literature. Likewise, no correction factors were applied to estimate the number of sea lions that were using haul-out sites off southern Vancouver Island, British Columbia, and that would forage in the same marine area as the sea lions that were using haul-out sites in northwest Washington.

We divided our total consumption estimate by 1000 to convert our estimate from kilograms to metric tons.

Table 1

Summary of the sampling of scat of Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) conducted from 2010 through 2013 in northwest Washington, by year, season, and month.

		No. of samples												
		Spring			Summer			Fall			Winter			
Species	Year	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Total
Steller sea lion	2010	0	0	0	0	0	32	3	0	27	0	0	0	62
	2011	48	18	24	35	36	42	4	31	36	0	38	0	312
	2012	38	35	34	28	36	38	35	22	38	8	0	39	351
	2013	0	0	0	0	0	0	0	0	0	0	34	17	51
California sea lion	2010	0	0	0	0	0	0	42	0	0	0	0	0	42
	2011	0	0	47	2	0	0	0	0	51	0	0	0	100
	2012	0	0	0	48	0	0	51	22	0	0	0	0	121

Monte Carlo simulations were used to incorporate uncertainty in estimating prey consumption by California and Steller sea lions. In each run of the model, parameter values were randomly selected from the parameter sampling distributions listed in Supplementary Table 2 (online only) for California sea lions and in Supplementary Table 3 (online only) for Steller sea lions. The simulation was run in R 10,000 times to estimate the mean and standard deviation (SD) of the total mass of prey consumed by California and Steller sea lions. We developed and used R code for estimating prey consumption by sea lions (the code is available from website).

We multiplied our seasonal prey consumption estimates by the SSFO of each prey taxon to estimate the average metric tons eaten by sea lions in each season. Because we had no winter diet data for California sea lions, we used the pooled SSFO from all scat collections to estimate the amount eaten in winter. Seasonal estimates were added together to obtain annual consumption of each prey type by each sea lion species.

Results

During the study, 776 scat samples from Steller sea lions and 263 scat samples from California sea lions were collected (Table 1). Collections of scat of Steller sea lions were conducted primarily at the Tatoosh Complex in winter, Sea Lion Rock in summer, and a mix of all sites in spring and fall (Suppl. Table 4) (online only). The majority of scats from California sea lions were collected at East Bodelteh Island, with 2 collections totaling 13 samples taken at Carroll Island. All raw count data from haul-out surveys and results from scat analysis are publicly available (Scordino et al.[6]).

Counts of sea lions

Counts indicate very different patterns in utilization of haul-out sites by California and Steller sea lions in northwest Washington (Fig. 2). Steller sea lions were present throughout the year with slightly greater counts in fall and slightly lower counts in winter. The greatest counts of California sea lions were recorded in fall. The proportion of the population of Steller sea lions composed of adult males, adult females, juveniles, and pups was variable by month, with adult females and juveniles accounting for the majority of counts (Fig. 3). The exception was during summer when males composed a percentage of the hauled-out population similar to that for adult females. For individual haul-out sites within the study area, counts reveal variable patterns in utilization by sea lion species (Suppl. Figs. 1–7) (online only) and by demographic group of Steller sea lions (Suppl. Figs. 8–14) (online only).

Diet of Steller sea lions

The primary prey groups (those with SSFO >5%) for all scat samples from Steller sea lions were Clupeidae (22.7%), Sebastidae (14.0%), Rajidae (13.1%), Salmonidae (11.7%), Pleuronectiformes (9.7%), Squalidae (8.3%), and Merlucciidae (5.6%) (Table 2).

For Steller sea lions, diet varied between seasons both in the SSFO of common prey species and diet diversity indices. Diet diversity was similar in spring and fall and in summer and winter, with the greatest diversity occurring in spring and fall for all measures (Table 3). The Levin's niche breadth values are likely driven by the fact that the 3 most common prey families in the spring and fall made up 47.5% and 47.1% of the Steller sea lion diet, respectively; whereas, the 3 most common prey families in the summer and winter made up 62.6% and 61.4% of the diet, respectively (Table 2). Pacific hake (*Merluccius productus*) were common in the summer (10.8%) and fall (8.5%) but rarely consumed in the

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[6] Scordino, J., A. Akmajian, and S. Riemer. 2021. Steller and California sea lion count and diet data in northwest Washington, 2010–2013. Mendeley Data, V1. [Available from website.]

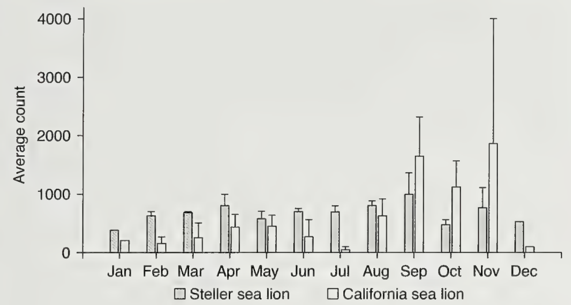

Figure 2

Average monthly counts of age-1+ Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*) in northwest Washington during vessel- and land-based surveys conducted from 2010 through 2013. Error bars indicate standard deviations.

winter (0.3%) and spring (0.9%). Conversely, consumption of Gadidae was low in the summer (1.7%) and fall (3.6%) but common in the winter (5.7%) and spring (9.0%). Pleuronectiformes were common in all seasons (>5%) except winter. Clupeidae was the most common prey family in the diet of Steller sea lions in summer with an SSFO of 36.7% but accounted for only 13.8% of the diet in spring, likely driven by the presence of Pacific sardine (*Sardinops sagax*), which had an SSFO of 18.5% in summer but was rarely consumed in other seasons.

Annual comparisons of diet included only data from 2011 and 2012 because samples were collected in all seasons (Table 1). Diet diversity was greater in 2012 than in 2011 for both measures (Table 3). Consumption of common prey species also varied between years. The SSFO of Clupeidae declined from 27.9% in 2011 to 20.1% in 2012, likely due to a large reduction in the consumption of Pacific sardine. From 2011 to 2012, the consumption of northern anchovy (*Engraulis mordax*) and Pacific hake also declined. In 2012, Steller sea lions had higher consumption of common prey taxa, including Pleuronectiformes, Salmonidae, and Pacific spiny dogfish (*Squalus suckleyi*), and increases in consumption of a number of less common prey taxa, in comparison to levels in 2011 (Suppl. Table 5) (online only).

Diet of California sea lions

The primary prey families (>5% SSFO) for all scat samples from California sea lions were Clupeidae (38.2%),

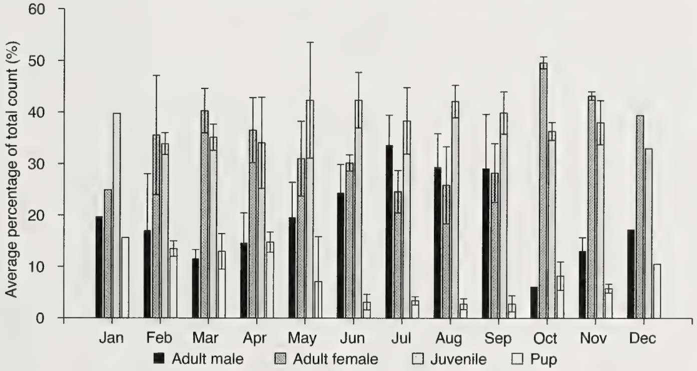

Figure 3

Average monthly percentage of counts of Steller sea lions (*Eumetopias jubatus*) at haul-out sites during 2010–2013 in northwest Washington for 4 demographic groups. The demographic groups used in counts were adult males, adult females, juveniles, and pups. Error bars indicate standard deviations.

Table 2

Split-sample frequency of occurrence (SSFO) and estimated metric tons (t) of prey consumed by major prey group (family, order, or class) and by the lowest identifiable taxonomic group (indented) for prey consumed by Steller sea lions (*Eumetopias jubatus*), based on examination of scat samples collected from 2010 through 2013 in northwest Washington. Numbers of different types of scat samples by season are also provided. The SSFO calculations for major prey groups and for the lowest identifiable taxonomic groups were performed separately and, as a result, produced slightly different values.

	Total		Spring		Summer		Fall		Winter	
Sample type					No. of samples					
Scat samples	776		197		247		196		136	
Samples containing identifiable prey	730		185		230		183		132	
Samples containing no identifiable prey	41		11		15		12		3	
Empty samples	5		1		2		1		1	
Prey consumption	11,327 t		2998 t		2039 t		3821 t		2469 t	
Prey group	SSFO	t	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Herrings, shads, sardines: family Clupeidae	22.7%	2573.8	13.8%	413.8	36.7%	747.6	21.0%	802.2	13.3%	329.0
Clupeids, unidentified	11.3%	1278.3	9.3%	278.2	15.2%	309.4	10.7%	409.0	8.1%	200.6
Pacific sardine (*Sardinops sagax*)	6.6%	748.5	0.0%	0.0	18.5%	378.1	3.0%	113.2	0.1%	3.1
Pacific herring (*Clupea pallasii*)	3.9%	440.5	2.6%	79.4	3.0%	60.9	6.2%	236.0	4.0%	99.5
American shad (*Alosa sapidissima*)	1.3%	144.6	1.9%	57.0	0.1%	2.2	1.9%	73.8	1.5%	37.7
Rockfishes: family Sebastidae	13.9%	1579.6	17.9%	537.4	8.3%	168.3	8.5%	325.8	25.8%	637.0
Rockfishes (*Sebastes* spp.)	13.8%	1567.0	17.7%	531.7	8.2%	168.0	8.4%	319.6	25.7%	634.6
Skates: family Rajidae	13.1%	1480.8	15.8%	473.0	9.2%	186.6	10.7%	407.2	19.5%	480.6
Skates, unidentified	12.7%	1442.6	15.5%	463.2	8.8%	179.4	10.2%	388.8	19.3%	477.6
Salmon: family Salmonidae	11.7%	1329.5	12.6%	377.1	5.8%	117.9	15.4%	588.9	15.8%	391.1
Salmon or trout, unidentified	11.6%	1315.4	12.6%	377.1	5.7%	116.1	15.1%	577.6	15.7%	388.0
Flatfishes: order Pleuronectiformes	9.7%	1100.5	8.8%	264.0	15.0%	305.9	10.1%	385.3	1.3%	31.4
Starry flounder (*Platichthys stellatus*)	4.4%	492.9	4.1%	123.4	6.9%	140.7	4.4%	167.7	0.2%	4.7
Righteye flounders, family Pleuronectidae	2.0%	225.4	1.8%	55.1	2.3%	46.0	3.0%	113.7	0.4%	9.4
Arrowtooth flounder (*Atheresthes stomias*)	1.3%	152.6	1.0%	29.4	3.2%	64.9	0.4%	14.6	0.0%	0.0
Flatfishes, unidentified	0.9%	97.1	0.7%	19.9	1.2%	25.1	0.9%	33.8	0.4%	10.9
Butter sole (*Isopsetta isolepis*)	0.6%	70.0	0.5%	14.0	1.1%	23.0	0.6%	21.8	0.0%	0.0
Rex sole (*Glyptocephalus zachirus*)	0.3%	38.9	0.0%	0.0	0.6%	11.5	0.6%	23.1	0.1%	1.9
Sanddabs (*Citharichthys* spp.)	0.3%	30.0	0.2%	7.3	0.2%	4.4	0.5%	20.6	0.0%	0.0
English sole (*Parophrys vetulus*)	0.2%	27.4	0.6%	18.9	0.0%	0.0	0.3%	10.4	0.1%	1.9
Dover sole (*Microstomus pacificus*)	0.2%	26.1	0.4%	13.2	0.2%	3.5	0.1%	3.5	0.2%	5.6
Sand sole (*Psettichthys melanostictus*)	0.1%	8.3	0.3%	8.6	0.0%	0.0	0.0%	0.0	0.0%	0.0
Slender sole (*Lyopsetta exilis*)	0.1%	6.5	0.0%	0.0	0.2%	3.7	0.0%	0.0	0.0%	0.0
Turbots (*Pleuronichthys* spp.)	<0.1%	3.9	0.0%	0.0	0.0%	0.0	0.1%	5.2	0.0%	0.0
Dogfish sharks: family Squalidae	8.3%	944.4	10.4%	311.3	5.6%	113.5	9.3%	355.5	9.0%	221.2
Pacific spiny dogfish (*Squalus suckleyi*)	8.2%	933.4	10.4%	310.5	5.5%	112.3	9.1%	347.0	8.9%	219.0
Hakes: family Merlucciidae	5.9%	663.7	0.9%	26.2	10.9%	222.2	8.6%	329.0	0.3%	6.2
Pacific hake (*Merluccius productus*)	5.8%	655.0	0.9%	26.2	10.8%	219.9	8.5%	322.9	0.3%	6.2
Cods: family Gadidae	4.8%	540.0	9.0%	270.4	1.7%	35.3	3.6%	138.6	5.7%	140.2
Cods, unidentified	2.1%	234.0	3.5%	105.1	0.6%	12.4	1.7%	65.8	3.1%	75.6
Walleye pollock (*Gadus chalcogrammus*)	1.4%	154.4	5.1%	152.6	0.0%	0.0	0.3%	11.1	0.0%	0.0
Pacific cod (*Gadus macrocephalus*)	1.2%	141.2	0.4%	10.5	1.0%	20.2	1.6%	60.0	2.5%	61.6
Pacific tomcod (*Microgadus proximus*)	<0.1%	3.9	0.0%	0.0	0.1%	2.2	0.0%	0.0	0.0%	0.0
Anchovies: family Engraulidae	2.1%	234.6	2.1%	62.0	1.9%	39.2	2.8%	107.9	1.3%	32.0
Northern anchovy (*Engraulis mordax*)	2.0%	230.5	2.1%	62.0	1.8%	37.7	2.8%	105.8	1.3%	32.0
Greenlings: family Hexagrammidae	1.7%	191.7	2.2%	64.6	0.6%	12.9	2.6%	99.6	1.6%	40.2
Lingcod (*Ophiodon elongatus*)	1.1%	124.7	2.1%	63.7	0.6%	11.4	1.3%	49.5	0.3%	8.4
Hexagrammids, unidentified	0.4%	48.9	0.0%	0.0	0.0%	0.0	0.8%	30.3	1.3%	31.8
Atka mackerel (*Pleurogrammus monopterygius*)	0.1%	14.7	0.0%	0.0	0.0%	0.0	0.5%	19.8	0.0%	0.0
Squids and octopuses: class Cephalopoda	1.1%	129.5	0.8%	23.9	0.4%	8.1	2.2%	82.9	1.5%	37.1
Squids and octopuses, unidentified	0.8%	89.6	0.5%	14.5	0.2%	3.7	1.5%	58.3	1.3%	31.3

(*Continued on next page*)

Table 2 *(continued)*

	Total		Spring		Summer		Fall		Winter	
Prey group	SSFO	t	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Octopuses, unidentified	0.2%	24.7	0.1%	4.1	0.2%	4.4	0.5%	17.6	0.0%	0.0
Squids, unidentified	0.1%	13.9	0.2%	5.4	0.0%	0.0	0.2%	6.5	0.2%	4.7
Sand lances: family Ammodytidae	1.0%	112.5	1.1%	33.5	0.9%	18.0	0.7%	28.0	1.4%	33.8
Pacific sand lance (*Ammodytes hexapterus*)	1.0%	111.8	1.1%	33.5	0.9%	17.6	0.7%	28.0	1.4%	33.8
Lampreys: family Petromyzontidae	0.8%	91.8	1.0%	29.3	0.4%	7.4	1.0%	40.0	1.0%	25.4
Lampreys, unidentified	0.5%	56.1	0.5%	16.2	0.4%	7.4	0.7%	26.1	0.4%	10.0
Pacific lamprey (*Entosphenus tridentatus*)	0.3%	35.2	0.4%	13.1	0.0%	0.0	0.4%	13.9	0.6%	14.8
Mackerels and tunas: family Scombidae	0.6%	68.5	0.0%	0.0	1.7%	34.7	0.3%	10.4	0.0%	0.0
Pacific chub mackerel (*Scomber japonicus*)	0.6%	65.2	0.0%	0.0	1.6%	32.8	0.3%	10.4	0.0%	0.0
Smelts: family Osmeridae	0.6%	65.0	0.5%	15.9	0.1%	2.2	1.0%	39.7	0.8%	19.8
Smelts, unidentified	0.6%	65.0	0.5%	15.9	0.1%	2.2	1.0%	39.7	0.8%	19.8
Eulachon (*Thaleichthys pacificus*)	<0.1%	1.9	0.0%	0.0	0.0%	0.0	0.0%	0.0	0.1%	2.3
Sticklebacks: family Gasterosteidae	0.4%	50.6	1.5%	46.5	0.0%	0.0	0.1%	5.2	0.1%	2.7
Threespine stickleback (*Gasterosteus aculeatus*)	0.4%	50.3	1.5%	46.5	0.0%	0.0	0.1%	5.2	0.1%	2.3
Poachers: family Agonidae	0.4%	45.8	0.5%	16.2	0.4%	8.9	0.3%	12.9	0.3%	6.2
Poachers, unidentified	0.3%	34.9	0.4%	12.2	0.4%	8.0	0.1%	5.6	0.3%	6.2
Sturgeon poacher (*Podothecus accipenserinus*)	<0.1%	3.1	0.0%	0.0	0.0%	0.0	0.1%	4.2	0.0%	0.0
Sculpins: family Cottidae	0.4%	42.6	0.4%	11.3	0.0%	0.0	0.7%	25.6	0.6%	15.3
Sculpins, unidentified	0.3%	36.2	0.4%	11.3	0.0%	0.0	0.5%	18.3	0.6%	14.2
Pacific staghorn sculpin (*Leptocottus armatus*)	<0.1%	5.2	0.0%	0.0	0.0%	0.0	0.2%	7.0	0.0%	0.0
Snailfishes: family Liparidae	0.3%	33.6	0.4%	10.8	0.4%	8.1	0.2%	7.0	0.2%	4.7
Snailfishes, unidentified	0.3%	29.5	0.2%	7.3	0.4%	7.7	0.2%	7.0	0.2%	4.7
Hagfishes: family Myxinidae	0.2%	17.9	0.4%	10.8	0.0%	0.0	0.2%	7.2	0.1%	2.7
Pacific hagfish (*Eptatretus stoutii*)	0.2%	17.1	0.4%	10.8	0.0%	0.0	0.2%	6.5	0.1%	2.3
Gunnels: family Pholidae	0.1%	10.3	0.0%	0.0	0.0%	0.0	0.0%	0.0	0.5%	12.5
Gunnels, unidentified	0.1%	10.3	0.0%	0.0	0.0%	0.0	0.0%	0.0	0.5%	12.5
Eelpouts: family Zoarcidae	0.1%	6.9	0.0%	0.0	0.0%	0.0	0.2%	9.3	0.0%	0.0
Eelpouts, unidentified	0.1%	6.9	0.0%	0.0	0.0%	0.0	0.2%	9.3	0.0%	0.0
Jacks: family Carangidae	<0.1%	5.2	0.0%	0.0	0.0%	0.0	0.2%	7.0	0.0%	0.0
Jack mackerel (*Trachurus symmetricus*)	<0.1%	5.2	0.0%	0.0	0.0%	0.0	0.2%	7.0	0.0%	0.0
Frogs and salamanders, class Amphibia	<0.1%	4.3	0.0%	0.0	0.0%	0.0	0.2%	5.8	0.0%	0.0
Frogs and salamanders, unidentified	<0.1%	4.3	0.0%	0.0	0.0%	0.0	0.2%	5.8	0.0%	0.0
Wolffishes: family Anarhichadidae	<0.1%	3.9	0.0%	0.0	0.1%	2.2	0.0%	0.0	0.0%	0.0
Wolf-eel (*Anarrhichthys ocellatus*)	<0.1%	3.9	0.0%	0.0	0.1%	2.2	0.0%	0.0	0.0%	0.0

Salmonidae (13.5%), Merlucciidae (11.3%), Sebastidae (9.3%), Squalidae (7.8%), and Engraulidae (5.0%) (Table 4).

For California sea lions, diet diversity was similar in spring and summer, but the diet was less diverse in fall (Table 3). There were large differences in the SSFO of some prey families between seasons. The 3 most dominant families of prey made up 58.6% of the diet of California sea lions in spring, 55.3% of the diet in summer, and 77.7% of the diet in fall. Consumption of Sebastidae dramatically declined in the fall to an SSFO of 2.0% from 20.5% and 22.8% in the spring and summer, respectively. Cephalopoda composed a primary prey group during spring (6.3%) and summer (8.4%) but were only 1.6% of the diet in fall. During the fall, 47.4% of the California sea lion diet was composed of Clupeidae, compared with 24.6% in spring and 20.5% in summer. Higher consumption of Clupeidae in the fall appears to be due to the consumption of Pacific sardine, which had an SSFO of 11.4% in the fall and was not present in the spring or summer.

For yearly comparisons of the diet of California sea lions, we used only data collected during the fall because samples were not collected in all seasons of each study year (Suppl. Table 6) (online only). Prey diversity was similar between years during the fall (Table 3). The SSFO of prey taxa varied between years. Consumption of Pacific hake declined from 23.4% and 18.0% of the diet in 2010 and 2011, respectively, to 4.6% in 2012, and consumption of northern anchovy declined from 10.7% and 7.1% of the diet in 2010 and 2011 to 2.2% in 2012. As the SSFO of Pacific hake and northern anchovy declined, California sea lions ate more Clupeidae (41.7% in 2010 versus 51.0% in 2012), such as Pacific sardine and American shad (*Alosa sapidissima*). Consumption by California sea lions of Salmonidae also increased each year during the fall from 11.6% of the diet in 2010 to 16.4% of the diet in 2012.

Table 3

Shannon–Wiener diversity index and Levin's niche breadth for prey of Steller sea lions (*Eumetopias jubatus*) (SSL) and California sea lions (*Zalophus californianus*) (CSL), within season and year, from examination of scat samples collected during 2010–2013 in northwest Washington. Corresponding 95% bias-corrected and accelerated bootstrap confidence intervals are provided in parentheses. Seasonal values are for samples collected during that season pooled across all years of study. Yearly values reflect all samples collected for all seasons pooled within that year.

Species	Period	Shannon–Wiener index	Levin's niche breadth
SSL	Spring	2.32 (2.27–2.40)	8.32 (7.87–8.96)
SSL	Summer	2.04 (1.97–2.13)	5.22 (4.68–5.87)
SSL	Fall	2.40 (2.34–2.49)	8.60 (8.00–9.44)
SSL	Winter	2.11 (2.03–2.24)	6.26 (5.69–7.01)
SSL	2011	2.23 (2.18–2.30)	7.00 (6.47–7.60)
SSL	2012	2.36 (2.32–2.44)	8.29 (7.90–8.83)
CSL	Spring	2.20 (2.10–2.34)	6.99 (6.01–8.40)
CSL	Summer	2.12 (2.04–2.25)	6.90 (6.09–8.21)
CSL	Fall	1.77 (1.67–1.90)	3.68 (3.17–4.24)
CSL	Fall 2010	1.66 (1.51–1.95)	3.88 (3.15–5.13)
CSL	Fall 2011	1.64 (1.48–1.83)	3.58 (2.84–4.49)
CSL	Fall 2012	1.76 (1.60–1.97)	3.34 (2.72–4.12)

Dietary niche overlap

The Morisita–Horn index indicates significant dietary niche overlap between Steller and California sea lions. Using data from spring, summer, and fall pooled for all years of the study, we found significant dietary niche overlap between these species of sea lions (MH=0.88; 95% confidence interval [CI]: 0.85–0.91). Data pooled by season indicate significant overlap in spring (MH=0.82; 95% CI: 0.75–0.89), summer (MH=0.76; 95% CI: 0.66–0.86), and fall (MH=0.76; 95% CI: 0.69–0.83). There was also significant dietary niche overlap between the diets of California and Steller sea lions by year (pooling of all samples collected in spring, summer, and fall), with an MH of 0.77 in 2010 (95% CI: 0.65–0.91), an MH of 0.94 in 2011 (95% CI: 0.92–0.97), and an MH of 0.82 in 2012 (95% CI: 0.76–0.88).

Prey consumption

The average annual amount of prey consumed by Steller sea lions and California sea lions hauling out in northwest Washington from 2010 through 2013 was 11,327 t (SD 1600) and 9063 t (SD 4098), respectively. The amount of consumption was variable by season for both species; California sea lions had much higher consumption in fall than in other seasons (Fig. 4). In Tables 2 and 4, we report prey consumption by prey group and by lowest taxonomic group identified.

Discussion

Diet characterization

This study is the first one to describe the diets of California and Steller sea lions in northwest Washington. Like in past studies, we found that California and Steller sea lions eat diverse assemblages of prey that are seasonally and annually variable (Bailey and Ainley, 1981; Lowry et al., 1991; Merrick et al., 1997; Reimer and Brown[1]; Sinclair and Zeppelin, 2002; Weise and Harvey, 2008; Womble et al., 2009; Scordino[2]; Orr et al., 2011; Riemer et al., 2011; Waite et al., 2012; Sinclair et al., 2013; Wiles, 2015; Trites and Rosen[3]). Steller and California sea lions in northwest Washington have diets among the more diverse that have been reported for these species on the basis of diet diversity indices (Aurioles-Gamboa and Camacho-Ríos, 2007; Orr et al., 2011; Waite et al., 2012; Sinclair et al., 2013).

We expected seasonal fluctuations in the diets of Steller and California sea lions for migratory prey taxa, such as the Pacific hake, the Pacific sardine, and Pleuronectiformes (Eschmeyer et al., 1983; Demer et al., 2012; Malick et al., 2020), but other seasonal fluctuations in their diets were a surprise. Resident, nonmigratory prey taxa, such as Rajidae and Sebastidae, composed a larger portion of the sea lion diets in winter and spring than in summer and fall, likely a result of compensation for the reductions of seasonally available prey. We expected to see a marked increase in consumption of salmon during the summer and early fall when adult Salmonidae migrate through the project area to their natal rivers (Weitkamp and Neely, 2002; Weitkamp, 2010), as observed in other

Table 4

Split-sample frequency of occurrence (SSFO) and estimated metric tons (t) of prey consumed by major prey group (family, order, or class) and by the lowest identifiable taxonomic group (indented) for prey consumed by California sea lions (*Zalophus californianus*), based on examination of scat samples collected from 2010 through 2013 in northwest Washington. Numbers of different types of scat samples by season are also provided. The SSFO calculations for major prey groups and for the lowest identifiable taxonomic groups were performed separately and, as a result, produced slightly different values. The total annual prey consumption was calculated by multiplying the SSFO pooled across spring, summer, and fall by the total prey consumption estimate, including the winter estimate of 553 t.

	Total		Spring		Summer		Fall	
Sample type	No. of samples							
Scat samples	263		47		50		166	
Samples containing identifiable prey	251		46		47		158	
Samples containing no identifiable prey	9		1		3		5	
Empty samples	3		0		0		3	
Prey consumption	9063 t		1551 t		1267 t		5692 t	
Prey group	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Herrings, shads, sardines: family Clupeidae	38.2%	3462.5	24.6%	382.2	20.5%	259.7	47.4%	2699.2
Pacific herring (*Clupea pallasii*)	13.5%	1219.4	12.0%	186.9	8.4%	107.0	15.4%	874.0
Clupeids, unidentified	13.0%	1181.4	10.0%	154.8	10.9%	138.6	14.5%	828.0
Pacific sardine (*Sardinops sagax*)	7.2%	652.1	0.0%	0.0	0.0%	0.0	11.4%	650.6
American shad (*Alosa sapidissima*)	6.1%	549.5	3.6%	55.4	1.4%	17.3	8.2%	466.0
Salmon: family Salmonidae	13.5%	1220.3	11.5%	178.7	13.9%	175.7	13.9%	791.7
Salmon or trout, unidentified	13.1%	1186.8	11.3%	175.3	13.8%	174.4	13.4%	763.8
Hakes: family Merlucciidae	11.3%	1026.7	9.1%	140.5	6.5%	82.9	13.4%	763.5
Pacific hake (*Merluccius productus*)	11.0%	996.7	8.9%	138.2	6.5%	82.9	12.9%	735.9
Rockfishes: family Sebastidae	9.3%	838.7	20.5%	317.5	22.8%	288.9	2.0%	111.4
Rockfishes (*Sebastes* spp.)	9.1%	829.1	20.0%	310.8	22.8%	288.3	1.9%	109.9
Skates: family Rajidae	1.9%	169.5	3.1%	48.4	3.1%	39.8	1.1%	64.2
Skates, unidentified	1.8%	162.2	2.8%	43.3	3.0%	38.4	1.1%	64.2
Dogfish sharks: family Squalidae	7.8%	702.6	9.4%	146.1	12.0%	151.6	6.0%	342.2
Pacific spiny dogfish (*Squalus suckleyi*)	7.6%	685.5	9.3%	143.9	12.0%	151.6	5.8%	327.6
Anchovies: family Engraulidae	5.0%	453.5	5.4%	84.3	1.9%	23.6	5.8%	330.8
Northern anchovy (*Engraulis mordax*)	4.8%	434.3	5.4%	84.3	1.8%	22.9	5.5%	312.6
Flatfishes: order Pleuronectiformes	4.0%	366.0	3.4%	53.4	5.7%	72.1	3.7%	211.7
Arrowtooth flounder (*Atheresthes stomias*)	1.5%	135.1	0.0%	0.0	3.1%	39.3	1.4%	82.3
Righteye flounders, family Pleuronectidae	0.9%	77.4	0.4%	5.6	0.3%	3.9	1.2%	66.0
Starry flounder (*Platichthys stellatus*)	0.7%	60.2	0.0%	0.0	2.1%	27.0	0.4%	24.0
Dover sole (*Microstomus pacificus*)	0.5%	49.3	1.2%	18.0	0.4%	5.4	0.4%	22.8
Sanddabs (*Citharichthys* spp.)	0.4%	34.3	1.0%	15.2	0.0%	0.0	0.3%	18.0
Flatfishes, unidentified	0.2%	21.7	1.1%	16.9	0.0%	0.0	0.1%	3.6
Rex sole (*Glyptocephalus zachirus*)	0.1%	7.2	0.4%	6.7	0.0%	0.0	0.0%	0.0
Squids and octopuses: class Cephalopoda	3.8%	341.9	6.3%	98.1	8.4%	107.0	1.6%	93.4
Squids and octopuses, unidentified	2.3%	210.1	4.1%	64.1	6.9%	87.4	0.4%	24.4
Octopuses, unidentified	1.1%	99.9	2.1%	32.3	1.5%	19.6	0.7%	39.0
Squids, unidentified	0.2%	15.6	0.0%	0.0	0.0%	0.0	0.3%	15.6
Cods: family Gadidae	1.9%	176.4	1.3%	19.7	3.6%	45.4	1.7%	94.3
Codfishes, unidentified	1.1%	102.3	1.2%	18.0	1.6%	20.7	1.0%	55.2
Pacific cod (*Gadus macrocephalus*)	0.5%	41.3	0.0%	0.0	1.4%	17.3	0.3%	18.0
Pacific tomcod (*Microgadus proximus*)	0.2%	14.4	0.0%	0.0	0.4%	5.4	0.1%	7.2
Walleye pollock (*Gadus chalcogrammus*)	0.1%	12.0	0.0%	0.0	0.0%	0.0	0.2%	12.0
Smelts: family Osmeridae	1.5%	136.4	1.3%	20.3	0.0%	0.0	2.0%	114.4
Smelts, unidentified	1.4%	129.1	1.3%	19.7	0.0%	0.0	1.9%	107.8
Eulachon (*Thaleichthys pacificus*)	<0.1%	3.6	0.0%	0.0	0.0%	0.0	0.1%	3.6
Greenlings: family Hexagrammidae	0.5%	48.1	1.1%	16.9	0.0%	0.0	0.5%	30.0
Lingcod (*Ophiodon elongatus*)	0.3%	30.1	1.1%	16.9	0.0%	0.0	0.2%	12.0
Hexagrammids, unidentified	0.1%	12.0	0.0%	0.0	0.0%	0.0	0.2%	12.0

(*Continued on next page*)

Table 4 (*continued*)

	Total		Spring		Summer		Fall	
Prey group	SSFO	t	SSFO	t	SSFO	t	SSFO	t
Eelpouts: family Zoarcidae	0.4%	36.1	2.2%	33.7	0.0%	0.0	0.0%	0.0
Eelpouts, unidentified	0.4%	36.1	2.2%	33.7	0.0%	0.0	0.0%	0.0
Sand lances: family Ammodytidae	0.2%	21.1	0.0%	0.0	1.2%	15.7	0.0%	0.0
Pacific sand lance (*Ammodytes hexapterus*)	0.2%	21.1	0.0%	0.0	1.2%	15.7	0.0%	0.0
Lampreys: family Petromyzontidae	0.2%	21.1	0.7%	11.2	0.0%	0.0	0.2%	9.0
Pacific lamprey (*Entosphenus tridentatus*)	0.2%	18.1	0.7%	11.2	0.0%	0.0	0.1%	6.0
Jacks: family Carangidae	0.2%	18.1	0.0%	0.0	0.0%	0.0	0.3%	18.0
Jack mackerel (*Trachurus symmetricus*)	0.1%	13.5	0.0%	0.0	0.0%	0.0	0.2%	13.5
Sculpins: family Cottidae	0.1%	9.0	0.0%	0.0	0.0%	0.0	0.2%	9.0
Sculpins, unidentified	0.1%	7.2	0.0%	0.0	0.0%	0.0	0.1%	7.2
Snailfishes: family Liparidae	0.1%	9.0	0.0%	0.0	0.0%	0.0	0.2%	9.0
Snailfishes, unidentified	0.1%	9.0	0.0%	0.0	0.0%	0.0	0.2%	9.0
Hagfishes: family Myxinidae	0.1%	6.0	0.0%	0.0	0.4%	4.5	0.0%	0.0
Pacific hagfish (*Eptatretus stoutii*)	0.1%	5.2	0.0%	0.0	0.3%	3.9	0.0%	0.0

pinniped studies (Womble et al., 2009; Walters et al., 2020). The diet of California sea lions generally met our expectation; whereas, the portion of Salmonidae in the diet of Steller sea lions was smaller in summer than in winter by a factor of 3.

Annual variability in the diets of both sea lion species were also observed. Large annual differences in the portion of the diet composed of Pacific sardine and Pacific hake were likely driven by environmental factors that affect their distribution (Demer et al., 2012; Malick et al., 2020). We had expected to see a large increase of Salmonidae in the diet of both sea lion species during 2011 because of the presence of odd-year pink salmon (*Oncorhynchus gorbuscha*), which contributed to the roughly 6 times more Salmonidae fish entering Puget Sound in 2011 than in 2012 (Losee et al., 2019). Despite higher availability of Salmonidae in 2011, the portion of diet composed of Salmonidae was slightly higher in 2012 than in 2011 for both sea lion species.

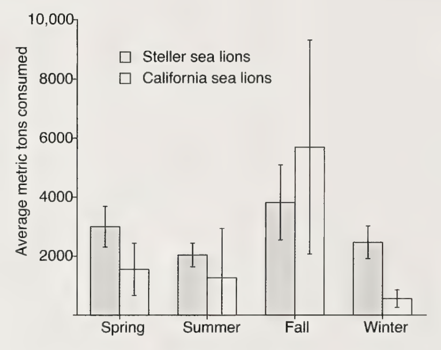

Figure 4

Estimated metric tons of prey consumed by Steller (*Eumetopias jubatus*) and California (*Zalophus californianus*) sea lions per season during 2010–2013 in northwest Washington. Error bars indicate standard deviations.

Pacific hake composed a smaller portion of the sea lion diets than expected. From their studies of California and Steller sea lion diets in Washington in the 1990s, Scordino[2] and Wiles (2015) reported that bones of Pacific hake had an FO of 89.0–98.0%, compared with an FO of 15.0% for Steller sea lions and an FO of 30.6% for California sea lion in our study (Suppl. Table 1) (online only). The large decrease over time in importance of Pacific hake in the diet of Steller sea lions was likely due to environmental factors that resulted in a smaller portion of the population of Pacific hake utilizing northwest Washington during our study (Malick et al., 2020). During 2010–2013, the period of our study, the Makah Tribe's commercial Pacific hake fishery, which is spatially restricted to northwest Washington within 40 nmi (74 km) of shore, also had lower than normal landings (Svec[7]). Low availability of Pacific hake likely resulted in greater consumption by both Steller and California sea lions of prey that are species of conservation concern, such as rockfish and salmon species.

Biases in our study method may have resulted in inaccuracies in our diet estimations. The annual and seasonal variability in diet may be an artifact of our sampling effort (Trites and Joy, 2005). We often had only 1 or 2 sampling occasions per season for California sea lions and between 1 and 6 sampling occasions per season for Steller sea lions, and this effort may have resulted in detecting short-term shifts in fish distributions and availability that were not representative of seasonal or annual trends. However, in a study of penguin diet, frequent samplings with small collections were compared to infrequent samplings with large collections, and no significant differences in diet estimates were found (Berrow et al., 1999). Additionally, we chose to use SSFO to document diet; however, other approaches, such as biomass reconstruction, have been proven to have more accurately reconstructed the diet of sea lions (Tollit et al., 2007). The use of SSFO in our study may have resulted in overreporting the importance of small-bodied prey and underreporting the importance of large-bodied prey (Laake et al., 2002; Tollit et al., 2007).

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[7] Svec, R. 2021. Personal commun. Makah Fish. Manage., Makah Tribe, 150 Resort Dr., Neah Bay, WA 98357.

Prey consumption

We estimated that Steller sea lions ate an average of 11,327 t (SD 1600) of prey per year and that California sea lions ate an average of 9063 t (SD 4098) of prey per year from 2010 through 2013 in northwest Washington. It is important when considering this result to remember that the scope of inference of this study was limited to sea lions hauled out in northwest Washington in 2010–2013. From 2010 through 2018, the average count of California and Steller sea lions hauled out in northwest Washington increased at a rate of 7.8% and 7.9%, respectively (Allyn and Scordino, 2020). At these observed rates of increase, our estimate of prey biomass consumed is likely less than half of what the 2 sea lion species are eating per year at the time of this publication.

Results from our model of consumption of prey by sea lions are best characterized as estimates rather than as definitive values for a number of reasons. First, we used published estimates for many parameters of the model. The proportion of body weight eaten per day published by Winship et al. (2006) is based on an energetic model with fixed caloric density of prey, although caloric densities are known to vary between species (Logerwell and Schaufler, 2005) and within species because of reproductive state and environmental factors (von Biela et al., 2019). Winship et al. (2006) did not account for fluctuations in caloric demands, but results from captive studies indicate that caloric demands of both Steller and California sea lions change seasonally (Kastelein et al., 1990, 2000).

We used haul-out count correction factors in our model that were developed for aerial surveys of sea lions (Lowry and Forney, 2005; Olesiuk[4]), although in our study, counts were conducted by vessel or from land. Vessel- and land-based counts are known to be negatively biased, compared to counts from aerial surveys (Westlake et al., 1997); however, no correction factor was available to compare values produced with our count method to aerial counts. We also did not account for the possibility that sea lions hauled out at sites in Canada, such as Carmanah Point, could forage in the same area as the sea lions hauled out in northwest Washington. Together, not accounting for the negative bias of vessel-based and land-based counts and not accounting for sea lions from Canada likely negatively biased our estimates of prey consumption for both sea lion species in our study area by an unknown amount. Despite the limitations and assumptions needed for our model of consumption, we believe it provided important perspective for the role of Steller and California sea lions in the northern California Current Ecosystem.

Dietary niche overlap

We hypothesized that Steller and California sea lions would have dietary niche overlap because they are central place foragers (Womble et al., 2009) that utilize the same haul-out sites (Mate, 1975) and have similar physiological dive limits (Weise et al., 2010). Our findings indicate that the sympatric sea lion species use the same dietary niche and are therefore competing for prey resources, but there are a number of caveats to this conclusion. First, interpreting niche overlap analyses is difficult because both a finding of no dietary niche overlap and a finding of significant dietary niche overlap could be signs of competition (Litvaitis et al., 1996). Further, significant overlap can occur without competition if prey species are abundant (Szabó and Meszéna, 2006). The observed rapid increase in counts of sea lions at haul-out sites in northwest Washington (Allyn and Scordino, 2020) indicates that prey resources were not limiting during our study.

Another consideration is that we evaluated dietary niche overlap by using prey grouped to family or a higher taxonomic order, an approach that assumes that prey species within groupings by family or higher taxonomic order represented prey items that were identical (Greene and Jaksić, 1983; Krebs, 1999). Some families of fish have species with very different behaviors, distributions, and sizes that affect their vulnerability to predation by the 2 sea lion species. For instance, in Sebastidae, there are species that are pelagic and schooling, solitary and benthic, primarily distributed in nearshore waters, and primarily distributed in offshore slope habitat (Eschmeyer et al., 1983). Even when we documented that the sea lions were eating the same species of prey, they could have exploited different size classes of that species. In a study in the Barents Sea, ringed seals (*Pusa hispida*) and harp seals (*Pagophilus groenlandicus*) had almost complete niche overlap strictly on the basis of identification of prey species in scat samples (Wathne et al., 2000), yet a closer examination of prey remains revealed niche partitioning with harp seals diving deeper for larger fish of the same species. Although our results indicate significant dietary niche overlap, it is possible that the sea lions of the 2 species in this study were partitioning their dietary niches in a way that our study design could not detect.

Conclusions

We found that Steller and California sea lions in northwest Washington have similar diets with seasonal and annual variability, and we found significant dietary niche overlap between the 2 species. Currently, there is no evidence that the dietary niche overlap between Steller and California sea lions is affecting the population growth of either species, but it bears monitoring if prey resources become limiting. Many of the prey species consumed by California and Steller sea lions during this study are culturally, economically, and ecologically important species (Kaplan and Leonard, 2012; Surma et al., 2018; Atlas et al., 2021). The estimates of prey consumption by the 2 sea lion species highlight the potential for increasing abundances of Steller and California sea lions in northwest Washington to result in reductions in the number of fish available to future recreational, commercial, and subsistence fisheries (Weise and Harvey, 2005, 2008; Chasco et al., 2017; Walters et al., 2020). Future diet studies conducted at a decadal scale would be useful for evaluating the effects of changing pinniped populations and ocean conditions.

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Characterizing spawning behavior of Greenland halibut (*Reinhardtius hippoglossoides*) in the eastern Bering Sea and Aleutian Islands

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Abstract—Understanding spawning behavior of commercial fish populations provides a basis for making management decisions related to these stocks. Archival tags can be used to define spawning behavior when depth-specific movements are involved. Spawning behavior of Greenland halibut (*Reinhardtius hippoglossoides*) in the eastern Bering Sea and the Aleutian Islands was inferred from archival tag data. The predominant period of identified spawning activity, based on abrupt vertical rises of females, occurred in January and February, and females reached apexes in their upward movement (*spawning rises*) at depths of approximately 200–350 m below the surface, indicating that the release of eggs could occur at depths shallower than previously assumed. Females had a single spawning rise annually, a result supporting the notion that this species is a total (single-batch) spawner. Male Greenland halibut exhibited spawning behavior, rises to shallower depths one or more times, for an average of 20 d. For large female Greenland halibut (>80 cm in fork length), spawning rises occurred in consecutive years, indicating that, despite oocyte development taking more than 1 year, spawning occurs annually. Inferring spawning behavior by using data collected with archival tags can aid in understanding the maturity of Greenland halibut.

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Archival tags can be attached to fish to collect environmental data, usually temperature and pressure (converted to depth) at a minimum, and individual events characterized by changes in such environmental conditions can be identified with data from recovered tags (Wilmers et al., 2015). The battery life of archival tags (also known as data storage tags) allows data to be recorded for up to several years, and the data therefore can be used to assess depth- or temperature-specific behavior, such as spawning, that occurs over annual cycles. Knowledge about reproductive traits (fecundity, maturity, and timing or location of spawning) of a fish stock is important for estimating the stock's reproductive potential (Murawski et al., 2001; Wright and Trippel, 2009; Cooper et al., 2013). Population estimates, mean weights by age, and maturity ogives (often derived from histological, macroscopic, or laboratory-based studies) are used for estimating stock reproductive potential in the form of spawning stock biomass (Marshall, 2009), although this measure is susceptible to size- and age-dependent effects (Trippel, 1999; Cooper et al., 2013). Misinterpretation of a reproductive trait can therefore lead to incorrect or biased estimation of stock reproductive potential.

Data from archival tags have been used to determine spawning behavior, allowing the unobservable to be "seen" (Seitz et al., 2005; Loher and Seitz, 2008; Murphy et al., 2017; Le Bris et al., 2018); therefore, this method can provide deductions of spawning behavior. In archival tag records, abrupt movements of fish to shallower depths are identified as *spawning rises*. These ascents are thought to be analogous to spawning behavior of shallow-water flatfish species that has been directly observed when they swim off the bottom to spawn (e.g., Manabe and Shinomiya, 2001). The rhythmic behavior of *batch spawning*, which refers to the behavior of species that spawn a batch of eggs every few days over a period of weeks, can be identified in archival tag data. Spawning rises have been inferred for 2 batch-spawning species, the Pacific halibut (*Hippoglossus stenolepis*) and the Atlantic halibut (*H. hippoglossus*), by using archival tags.

Although female halibut are expected to have multiple spawning rises separated by at least 2 days, during which time batches of ova are hydrated (St-Pierre, 1984; Finn et al., 2002), male halibut are limited only by mating opportunities, resulting in a pattern in which spawning rises are more variable and frequent. In previous studies, data from archival tags was used to reveal spawning rises in females (e.g., one Pacific halibut rose 7 times in 3 weeks), and the authors also hypothesized that male spawning behavior had a more frequent and variable rise pattern, although sex was not identified (Seitz et al., 2005; Loher and Seitz, 2008). Similar patterns of spawning behavior of Atlantic halibut have been discerned in archival tag data with sex determined: female spawning has been characterized by 4–6 rises over a period of 10–17 d, and males have been reported to have more sporadic rises over a protracted period (Murphy et al., 2017).

The Greenland halibut (*Reinhardtius hippoglossoides*), also known as the Greenland turbot, is a close relative to the Pacific and Atlantic halibut (Vinnikov et al., 2018) and is a commercially important deepwater flatfish species found in the North Atlantic, North Pacific, and Arctic Oceans. This species can reach a size of up to 120 cm in fork length (FL), and females become mature at 60–70 cm FL (Cooper et al., 2007). Adult Greenland halibut have been found at depths greater than 1500 m and in waters with temperatures from 0°C to 4°C (Peklova et al., 2012; Siwicke and Coutré, 2020). Archival tag data from other studies indicate that Greenland halibut exhibit much vertical activity (Boje et al., 2014; Siwicke and Coutré, 2020) and can spend up to a quarter of their time in the pelagic environment (Albert et al., 2012). This species carries 2 cohorts of vitellogenic oocytes that are easily separated by their relative diameters, large and small (Kennedy et al., 2011). Interpretations of this trait for Greenland halibut have evolved (e.g., Fedorov, 1968; Rideout et al., 1999; Gundersen et al., 2000; Junquera et al., 2003), but the most recent understanding is that oocytes take more than 1 year to complete vitellogenesis, 2 cohorts of oocytes are present, with the large cohort spawned in the current year and the small cohort spawned in the following year (Kennedy et al., 2011; Rideout et al., 2012). This reproductive trait has been found in other coldwater fish species (e.g., Everson, 1994).

One basic aspect of reproduction of Greenland halibut that is uncertain is whether females are batch or total spawners (Stene et al., 1999; Kennedy et al., 2009). Female Greenland halibut are often caught in a prespawning or postspawning stage, and ripe or running females are rare. A single running female readily released all of her ovulated eggs when artificially spawned (Stene et al., 1999), and another female Greenland halibut released a single batch of eggs over the course of a year in a laboratory (Domínguez-Petit et al., 2013); both of these outcomes indicate that the species is a total spawner. When ripe females have been caught during longline surveys near Greenland, all oocytes were hydrated (although it was not stated whether this finding was only for the large cohort of oocytes), indicating that Greenland halibut spawn a single batch in the wild (Gundersen et al., 2013). The term *total spawner* can be used to describe a Greenland halibut that releases eggs once in a year (Murua and Saborido-Rey, 2003).

Knowledge of the timing and location (spatial and depth) of spawning is important for understanding stock structure and dynamics (i.e., egg-larval drift and migrations), basic information used in stock assessment and fisheries management. For Greenland halibut, these characteristics appear to vary by region and are poorly understood. Spawning activity of Greenland halibut inferred from gonadosomatic index analyses indicates that spawning occurs along the continental slope from November through January (Albert et al., 2001). Larval distributions indicate that this species spawns at depths between 800 and 1000 m from December through April (Smidt, 1969). Serebryakov et al. (1992) determined that spawning occurs at depths between 1000 and 1500 m, using the presence of larvae at these depths. The majority of the spawning of Greenland halibut in the eastern Bering Sea is assumed to occur deep on the slope (Alton et al., 1988) and between October and March (October–December, Musienko, 1970; February–March, Bulatov, 1983; and December–January, Sohn et al., 2010). Archival tag data from another study indicate that this stock does move to deeper waters along the continental slope during winter, a shift that is presumed to be from feeding to spawning grounds (Siwicke and Coutré, 2020). In captivity, spawning has occurred mostly from January through March in consecutive years (Domínguez-Petit et al., 2013). It is difficult to know what effect the laboratory conditions had on reproduction.

The depth at which eggs are released influences egg dispersal (currents) and development time (temperature). Both development of the embryo and timing of hatching are dependent upon the surrounding water temperature (Domínguez-Petit et al., 2013). It is believed that, in the Bering Sea, spawning occurs in deep submarine canyons and eggs are advected up and onto the nursery grounds of the continental shelf (Sohn et al., 2010; Duffy-Anderson et al., 2013). The accuracy of these assumptions will influence the accuracy of estimated development time and hatch date. For example, if an egg was in water that is warmer than assumed, the development time would be shortened, the back-calculated hatch date would be later in the year, and the time for egg dispersal by currents would be shortened. Additionally, if the depth at which eggs are released is incorrect and if current speed varies by depth, estimates of dispersal distance of eggs will also be affected.

If spawning is identifiable in archival tag data, this method can be useful for corroborating estimates of size at maturity and other characteristics from stock assessments. Currently, the assessment of the Bering Sea–Aleutian Islands (BSAI) Greenland halibut stock uses a logistic relationship of maturity and size, with the length at 50% maturity (L_{50}) set at 60 cm (2% at 50 cm and 98% at 70 cm) following D'yakov (1982). Results of later work indicate a larger L_{50}, but the study had limited sample sizes and its L_{50} has not been adopted for stock assessments (Cooper et al., 2007). Following the acknowledgment that there are 2 separate cohorts of oocytes simultaneously developing (Kennedy et al., 2011), the large cohort to be spawned this year and the small cohort to be spawned in the following year, maturity ogives of 2 different stocks of Greenland halibut have been reanalyzed with the small cohort of oocytes considered to be immature. In analysis of archival tag data from work in eastern Greenland, reclassifying females as having only developing oocytes (i.e., only the first cohort of oocytes that will not be mature in 12 months) led to a decrease in the estimate of spawning stock biomass of an average of 56%, with associated declines in total egg production; notably, estimates of L_{50} increased from 63.8 to 80.2 cm FL for one stock and from 61.2 to 74.1 cm FL for the other (Kennedy et al., 2014). Lengths of tagged female Greenland halibut that exhibited spawning behavior could be used to inform decisions regarding maintaining or reexamining the L_{50} used in stock assessments.

Our objective was to assess whether we could identify spawning behavior in data from archival tags implanted in Greenland halibut, and if so, to characterize it. If spawning behavior can be detected in tag data, we could infer and clarify several aspects of the reproduction of Greenland halibut in the BSAI: 1) the timing of spawning, 2) the depth at which eggs are released, 3) the frequency of spawning in a year (i.e., batch or total), and 4) whether individual females spawn in consecutive years.

Materials and methods

Data collection

Archival tags have been implanted in Greenland halibut since 2003 during the longline surveys conducted by the NOAA Alaska Fisheries Science Center in the BSAI region. Briefly, longlines are set along the continental slope in the BSAI, and Greenland halibut captured on predetermined hooks that are in good condition and longer than 50 cm FL are placed in a tank with flowing seawater prior to tagging. The minimum length threshold of 50 cm FL meant that tagged fish were likely to be mature (Cooper et al., 2007).

A total of 297 Greenland halibut had Lotek[1] archival tags (Lotek Wireless Inc., Newmarket, Canada) internally implanted, with the specific tag model varying by year (2003: model LTD-1250; 2005–2008: model LTD-1300; 2011: model LAT-2800). Tags recorded temperature and pressure (converted to depth) at regular sampling frequencies between 1 and 15 min, depending on the year of deployment. The tag, surgical site, and tools were disinfected by using 3% Betadine, tags were inserted into the body cavity through a 2-cm-long incision made in the abdominal wall of the right side of the fish, and the incision was closed with surgical staples. Fish were released in close proximity to their site of capture, and tags were recovered by commercial fishing vessels (trawl or longline). Size (FL) of Greenland halibut was recorded at release, and FL, weight, and sex (determined with visual inspection of gonads) were recorded for some but not all tagged fish that were recaptured.

Identified spawning behavior

Archival tag data, specifically depths converted from pressure records, from tags implanted in Greenland halibut were used to identify and characterize the timing, depths, and frequency of spawning behavior for this species. Depth data were analyzed to find spawning behavior defined as "abrupt spikes," which consist of rapid ascents to an apex followed by rapid descents, as outlined in Seitz et al. (2005), Loher and Seitz (2008), and Murphy et al. (2017). We first filtered each fish's depth record to the most extreme 0.1% of ascents and descents to focus on a smaller more manageable subset (Suppl. Fig. 1) (online only). Larger percentages (>1% and >5%) were explored but did not add any insight into spawning behavior. In addition, spawning rises are expected to occur over periods of only hours to days in an individual's year. When an extreme ascent closely preceded an extreme descent, the entire depth record for that day was further analyzed. Greenland halibut may use more of the water column than Atlantic and Pacific halibut (e.g., Albert et al., 2012), and rapid ascents and descents could be related to other behaviors that are not related to spawning. Often, extreme ascents or descents were identified in isolation, or a descent was followed by an ascent; however, given our assumption that a spawning rise is a rapid ascent from the seafloor to spawn midwater followed by a rapid return to the seafloor, these other events were not further analyzed (Suppl. Fig. 2) (online only). Among flagged events, sex-specific similarities aided in deciding which events to classify as spawning behavior (e.g., Murphy et al., 2017).

The start date, time of day, and initial depth were identified for the time directly before the initiation of the first spawning rise, and the end date, time of day, and final depth were recorded at the completion of the last spawning rise, such that multiple rises would be encompassed in this period. The exact times when a rise was initiated and completed were determined on a case-by-case basis, by qualitatively and visually assessing the depth profile preceding and following rises to best capture the individual behavior. The time of day at which an individual reached a minimum depth during spawning rises (i.e., the apex) was noted to assess whether there was a daily preferred time of spawning. Additionally, the maximum ascent and descent rate (meters per minute) occurring between the start and end times of a spawning event were also compared.

Spawning rises of female Greenland halibut were further investigated to discern whether they occurred multiple times or singularly within a year and whether they occurred in consecutive years. We anticipated finding multiple rises over the course of several days if batch spawning was occurring, as has been observed for Atlantic halibut (Murphy et al., 2017). A singular rise would indicate total spawning, or a single batch, as has been observed for captive Greenland halibut (Domínguez-Petit et al., 2013). Evidence of female Greenland halibut having spawning rises in consecutive years (from tagged fish that were at liberty for more than 1 winter) would indicate that spawning can occur every year despite oocyte development requiring a period of 2 years (Kennedy et al., 2011; Rideout et al., 2012). Such a reproductive scenario is unusual but still considered that of a total spawner. In the first year, a female produces oocytes, but no spawning occurs. In the second and subsequent years, 2 cohorts of oocytes are present in the ovaries (a small cohort, with less than 1 year of development, and a large cohort, with more than 1 year but less than 2 years of development); the large cohort is spawned in the second year, and spawning can occur each subsequent year.

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[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

The depths of the apexes of spawning rises for female Greenland halibut were carefully estimated because these depths were assumed to be the depths at which eggs were released. Similar assumptions have been made for the family Pleuronectidae because the only observed flatfish spawning behavior has included release of eggs at the apex of spawning rises (see review in Seitz et al., 2005). Estimation of the apex depth varied with the sampling frequency of the tag, given that an increase in sampling frequency increases the probability of capturing the actual apex. When the sampling interval was 1 min, the minimum depth achieved was the estimate of the apex. For sampling intervals greater than 1 min (i.e., 4 and 15 min), depths were interpolated to a 1-min frequency by using the intersection of 2 simple linear models, the ascent and the descent. The estimated apex was determined by setting these equations equal to each other (i.e., the depth at which the 2 lines cross). This interpolation was not intended to exactly replicate the trajectory of these fish, although it was expected to approximate the depth of the apex better than taking the observed minimum depth from a low-frequency sampling interval (Suppl. Figs. 3 and 4) (online only). Additional information related to inferring and interpolating spawning rises is available in Supplementary Materials (online only).

Results

As of 2020, 22 of the 297 (7.4%) Greenland halibut implanted with archival tags have been recovered and returned to the Alaska Fisheries Science Center. The tags from 13 of these fish (6 males, 5 females, and 2 fish of undetermined sex) provided usable data through at least one presumed spawning period, October–March, with 6 fish at liberty for multiple years (Suppl. Table) (online only). Spawning behavior was identified and characterized for 11 tagged Greenland halibut (6 males, 3 females, and 2 fish of undetermined sex). Release and recapture locations were across the BSAI region (Fig. 1).

Extreme ascents and descents of tagged fish occurred throughout the year, but the top 0.1% of vertical movements

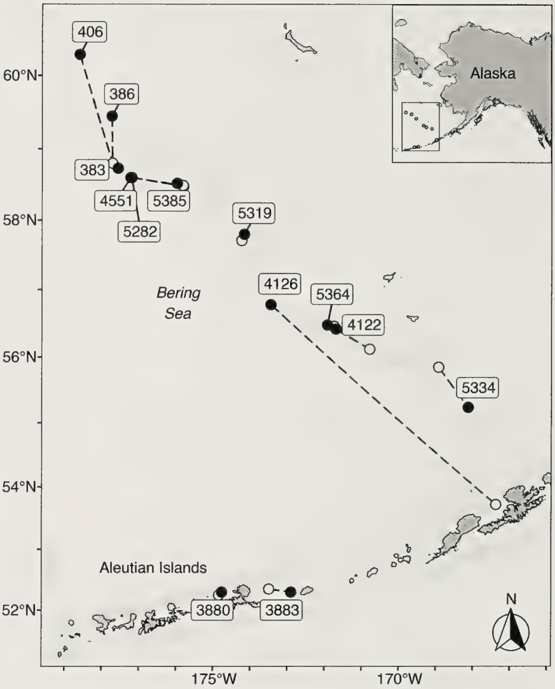

Figure 1

Map of the study area in the eastern Bering Sea and Aleutian Islands showing locations where Greenland halibut (*Reinhardtius hippoglossoides*) were tagged and released (gray circles) and later recovered (black circles). The tag numbers of recovered fish are provided for each location. Dashed lines indicate straight-line movement trajectories, and solid gray lines indicate isobaths at 200, 500, 1000, 1500, and 2000 m. The inset shows the location of the study area in relation to Alaska.

generally coincided with data for males and females during January and February (Suppl. Fig. 1) (online only). Upon closer inspection, numerous spawning rises were identified, with 2 distinct patterns that mostly varied with sex: 1) a singular rise with a sharp ascent and descent for females and 2) more sporadic, often prolonged periods of rapid ascents and descents for males (Fig. 2). Maximum ascent rates ranged from 8.1 to 31.0 m/min, with maximum descent rates between 10.5 and 28.0 m/min (Table 1).

Females

Three of the 5 female Greenland halibut had spawning rises and were 84–88 cm FL at release; the 2 that did not were 68 and 71 cm FL at release. The females that exhibited spawning behavior did so for all winters at liberty (Fig. 3). The dates of the singular rises by females ranged from 12 January to 12 February, with individuals having almost exactly a 1-year interval between rises (Table 1). Individual females initiated spawning rises from relatively similar depths across years (Table 1). The shallowest depths recorded for females at the apexes of their rises ranged from 229 to 420 m, and the narrower estimates from interpolation were between 217 and 326 m (Fig. 4). The elapsed time of singular rises ranged from 0.5 to 2.5 h. The duration of spawning rises generally lengthened with increases in the bottom depth at which ascents were initiated. No consistent pattern for the time of day at which fish reached an apex was observed (Table 1). Recorded temperatures were 2.8–3.8°C before spawning rises and 3.7–4.1°C at the apex of ascents. Because the tags were internally implanted and the ascents and descents were steep, tag sensors were unlikely to have adjusted to the ambient water temperature and the actual apex temperature was likely to have been warmer than tag data indicate. The movement of one fish (tag no. 386, with no spawning rises identified) is unique in that, during the winter, the fish moved to relatively shallow water, presumably to the continental shelf.

Males

All 6 male Greenland halibut exhibited spawning behavior during at least 1 winter for an average of 20 d. Four of these males were at liberty only for the winter of 2003–2004; for these males, spawning behavior occurred for 27–41 d between 2 January and 13 February (Table 1). One male was at liberty for 3 consecutive winters, and the data from its tag provides evidence of spawning behavior occurring in each year. In the third winter, this fish inhabited waters that were substantially deeper (depths of ~1200 m) than in the previous 2 winters (depths of 600–700 m), and it had a single, brief spawning rise to a depth of 508 m on

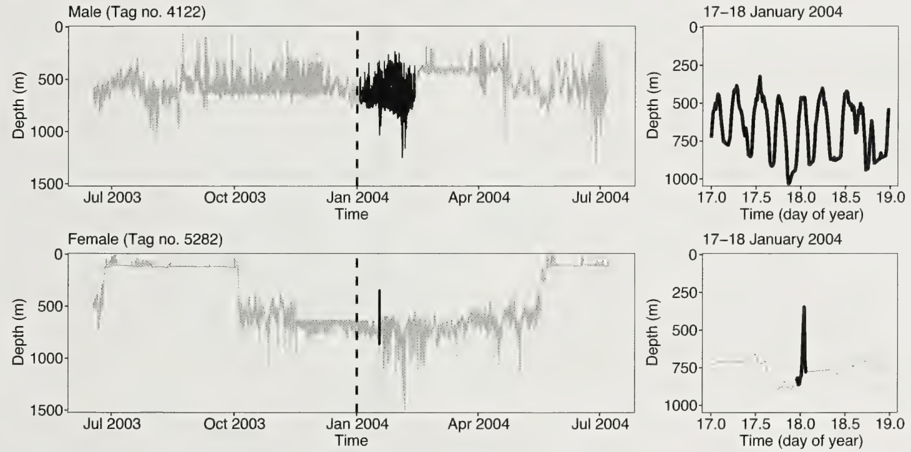

Figure 2

Examples of 1 year of depth data for a male (top left) and female (bottom left) Greenland halibut (*Reinhardtius hippoglossoides*) tagged and released in June 2003 in the eastern Bering Sea. The vertical black dashed line in each left panel indicates the change in year from 2003 to 2004, and the black parts of lines indicate the timing of putative spawning. The right panels focus on depth data for 2 d (17 and 18 January 2004), and this period is highlighted by a vertical grey bar in each left panel, with the black parts of lines again indicating the timing of associated spawning.

Table 1

Summary of data on putative spawning of Greenland halibut (*Reinhardtius hippoglossoides*) tagged in 2003, 2005, 2008, or 2011 and recaptured in the eastern Bering Sea and Aleutian Islands. Data collected include the tag number, year of spawning observation, sex of fish, day of the year spawning initiated (D_i), depth preceding minimum depth during spawning (Z_i), shallowest depth during spawning (Z_{min}), time at shallowest depth during spawning ($Time_{min}$), depth following minimum depth during spawning (Z_f), day of year spawning ended (D_f), elapsed time spawning occurred (Dur.), maximum spawning ascent rate (Asc_{max}), and maximum spawning descent rate (Des_{max}). Sex is presented for females (F), males (M), and those fish for which sex is undetermined (U), with a subscript indicating which sex it is likely to be on the basis of the archival tag data. Additional information on each tagged fish can be found in Supplementary Table (online only).

Tag no.	Year	Sex	D_i	Z_i (m)	Z_{min} (m)	$Time_{min}$	Z_f (m)	D_f	Dur. (d)	Asc_{max} (m/min)	Des_{max} (m/min)
5282	2004	F	18	859	347	0100	777	18	0.08	13.6	25.2
5282	2005	F	19	972	420	0800	895	19	0.10	19.7	25.6
5282	2006	F	17	886	343	1115	919	17	0.07	17.0	16.4
4551	2006	F	12	716	240	0132	716	12	0.05	19.8	23.3
4551	2007	F	13	917	254	0452	979	13	0.08	18.9	20.4
383	2012	F	43	619	229	2220	617	43	0.04	31.0	24.5
383	2013	F	26	526	240	1435	482	26	0.02	29.5	28.0
383	2014	F	25	527	230	1125	591	25	0.03	26.5	26.5
4122	2004	M	2	824	234	0345	820	44	41.43	15.2	10.5
4126	2004	M	10	1098	328	0430	1243	43	32.90	17.1	20.6
5319	2004	M	12	1435	239	0300	1438+	40	27.48	15.6	15.7
5364	2004	M	2	1489+	360	2130	1489+	40	37.82	17.2	17.9
5385	2004	M	6	689	221	0445	665	22	16.75	17.2	20.1
5385	2005	M	10	750	268	0245	708	34	23.73	15.8	11.9
5385	2006	M	8	1232	508	2300	1021	9	0.18	8.1	11.9
3883	2010	M	6	664	253	1716	670	6	0.07	24.0	14.3
5334	2004	U_M	2	956	266	0000	968	32	30.42	15.2	11.7
3880	2009	U_F	11	1520	310	1608	1361	11	0.20	17.5	20.3

8 January (Fig. 5). Another male, released and recaptured in the Aleutian Islands (tag no. 3883; Fig. 1), was at liberty for 2 winters, with tag data indicating that no spawning behavior occurred in the first winter and that a single spawning rise occurred in the second winter on 6 January (Table 1, Fig. 5). The shallowest recorded depths for males during spawning rises ranged from 221 to 508 m (Table 1). No effort was made to better estimate apexes when the sampling interval was greater than 1 min because males often had more staggered ascents and descents and lingered at shallow depths (<500 m), and as a result, the apexes of their ascents were not easily interpolated with linear methods. Temperature at the apexes ranged from 3.6°C to 4.3°C. Time of day varied for spawning rises (Table 1), and individuals had varying patterns in frequency and duration of their ascents (Fig. 5).

Fish of undetermined sex

For 2 fish with usable data, sex could not be determined at recapture, but spawning behavior was identified for both. One of these fish (tag no. 3880) was released and recaptured in the Aleutian Islands and exhibited behavior consistent with a singular spawning rise of a female; this distinction is not definitive because males sometimes had only a single ascent evident in their tag data. The release and recapture sizes of this fish were recorded as 94 cm FL, and sexually dimorphic size differences indicate that this fish is likely a female because females typically reach greater sizes than males (Bryan et al., 2018). The singular spawning rise of this fish occurred on 11 January, beginning at a depth of 1520 m and reaching a minimum depth of 310 m, before returning to a depth of 1361 m (Table 1, Fig. 6). The second fish (tag no. 5334) had a size of 69 cm FL recorded at release (no FL was recorded at recapture). This fish exhibited behavior with repetitive spawning rises between 2 January and 1 February (Table 1, Fig. 6), reaching a minimum depth of 266 m during this time. This spawning behavior was similar to that of known males in this study.

Discussion

Field-based tagging research on Greenland halibut can be used to infer previously unobserved reproductive behavior and is an important complement to lab-based research. The research of this study provides information for identification of spawning rises of Greenland halibut. Further, results of this work indicate distinct spawning behaviors for each sex: females have a single spawning rise, and males often make repetitive ascents over a protracted period. Findings from analysis of archival tag data

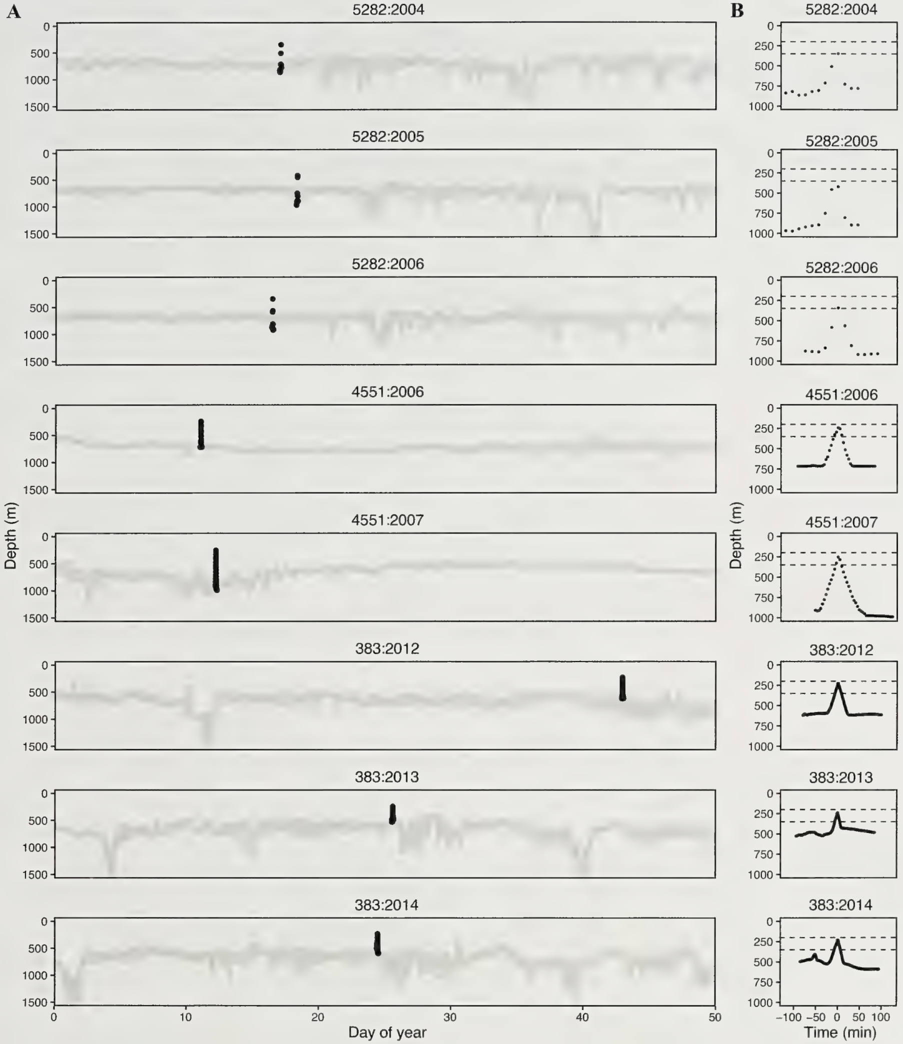

Figure 3

Putative *spawning rises*, meaning abrupt movements of fish to shallower depths, identified in archival tag data for 3 female Greenland halibut (*Reinhardtius hippoglossoides*) tagged in 2004, 2006, and 2012 (tag nos. 5282, 4551, and 383, respectively) in the eastern Bering Sea. (**A**) Tag-recorded depths of fish are provided for the first 50 d of the year (grey circles), with black circles indicating depths during spawning rises. Panel titles are the tag number and the year data were recorded (e.g., *5282:2004* means data recorded in 2004 for the fish implanted with tag no. 5282). (**B**) Close-ups of spawning rises that reached an estimated depth <400 m are provided, with the time for the minimum depth recorded set to 0 min to align all the rises. In each B panel, horizontal dashed lines at depths of 200 and 350 m are shown as references.

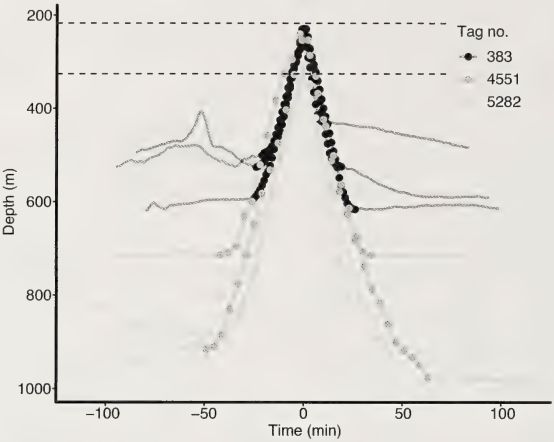

Figure 4

Putative *spawning rises*, meaning abrupt movements of fish to shallower depths, identified in archival tag data for 3 female Greenland halibut (*Reinhardtius hippoglossoides*) tagged in 2004, 2006, and 2012 (tag nos. 5282, 4551, and 383, respectively) in the eastern Bering Sea. Black and gray circles indicate depths recorded during spawning rises. Lines indicate depth profiles before, during, and after spawning rises and apexes of those rises (apexes were estimated by using simple linear models with data from tags with sampling intervals >1 min). The time at the apex of the rise has been set to 0 min, and horizontal dashed lines indicate the minimum and maximum depths estimated for the apex of putative spawning rises (217–326 m).

indicate that Greenland halibut in the BSAI region spawn from January through February, with eggs being released 217–326 m below the surface (inferred from interpolated apexes of spawning rises of females), although they normally inhabit deeper water. Because our study involved a small sample of individuals from the population and because tags recorded at intervals of 1–15 min, we believe that it is prudent to assume that eggs are released at a broader depth range of 200–350 m. The notions that Greenland halibut are total spawners and are capable of spawning annually are also supported by identification of singular spawning rises made by females in consecutive years. The depths at which females initiated spawning rises may provide evidence of depth (or site) fidelity. For example, a fish (tag no. 5282) began rises at depths of 859 m, 972 m, and 886 m in 3 consecutive years, and another fish (tag no. 383) initiated rises at depths of 619 m, 526 m, and 527 m in 3 consecutive years (Table 1).

The consistency in the time between annual spawning rises identified for females in this study was remarkably close to 1 year; therefore, the timing of spawning of an individual female likely can be predicted from the time it spawned the previous year. This hypothesis has been put forward for lumpfish (*Cyclopterus lumpus*), another species with this trait (Kennedy and Ólafsson, 2019). Consistency in the timing of spawning for the BSAI Greenland halibut stock indicates that spawn timing for populations in other regions should be reexamined. Considering that the 2-year oocyte development of this species was not well understood until recently (Kennedy et al., 2011; Rideout et al., 2012), it is possible that misspecification of maturity could lead to incorrect conclusions across the entire range of the Greenland halibut.

Temperature and currents may play a role in regulating development time and dispersal of the eggs and larvae of Greenland halibut. Greenland halibut are known to overwinter at depths >600 m (Siwicke and Coutré, 2020), in contrast to the depths where Pacific (<600 m) and Atlantic (<500 m) halibut overwinter (Loher and Seitz, 2008; Murphy et al., 2017), and the commonly held assumption is that Greenland halibut release their eggs at these depths (Alton et al., 1988; Sohn et al., 2010; Duffy-Anderson et al., 2013). Our results indicate that Greenland halibut may release eggs at depths that are much shallower than previously thought, possibly affecting interpretation of egg and larval incubation and distribution. Spawning rises identified for females in the winter consistently peaked just below the mixed layer, which in the Bering Sea is deeper and cooler during the winter than during other seasons, reaching depths of approximately 200 m; a permanent halocline exists below the maximum depth of the mixed layer, and the subsurface temperature maximum is centered at 200–300 m (Johnson and Stabeno, 2017).

Because embryo development of Greenland halibut, and therefore the timing of the hatch, depends upon water temperature (Domínguez-Petit et al., 2013) and because temperature is correlated with depth, back-calculations of spawn timing from egg and larval development can be incorrect if assumptions of the depth at which spawning occurs are wrong. Another large deepwater flatfish species, the Pacific halibut, it has been assumed, spawns on the bottom (Bailey et al., 2008), although evidence of spawning rises indicate that eggs are plausibly released at depths higher in the water column (Seitz et al., 2005; Loher and Seitz, 2008). Results of analysis of archival tag data indicate that similar misspecification of spawning depth may be occurring for Greenland halibut, and this problem should be resolved in future modeling efforts.

The sex-specific differences observed in the spawning behavior of Greenland halibut in this study indicate that females spawn a single batch when fully developed and

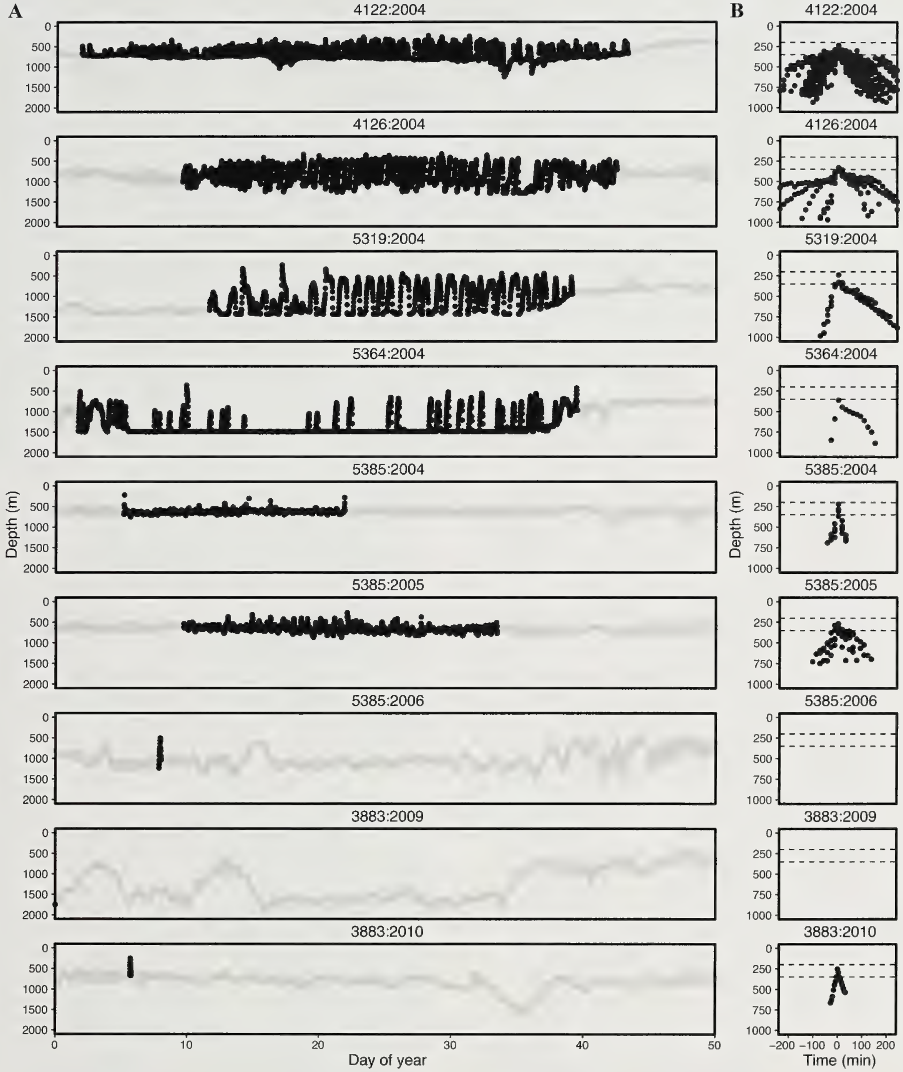

Figure 5

Putative *spawning rises*, meaning abrupt movements of fish to shallower depths, identified in archival tag data for 6 male Greenland halibut (*Reinhardtius hippoglossoides*) tagged in 2004 (tag nos. 4122, 4126, 5319, 5364, and 5385) and 2005 (tag no. 5385) in the eastern Bering Sea and in 2010 (tag no. 3883) in the Aleutian Islands. (**A**) Tag-recorded depths of fish are provided for the first 50 d of the year (grey circles), with black circles indicating depths during spawning rises. Panel titles are the tag number and the year data were recorded (e.g., *4122:2004* means data recorded in 2004 for the fish implanted with tag no. 4122). (**B**) Close-ups of spawning rises that reached a depth <400 m are provided, with the time for the minimum depth recorded set to 0 min to align all the rises. In each B panel, horizontal dashed lines at depths of 200 and 350 m are shown as references.

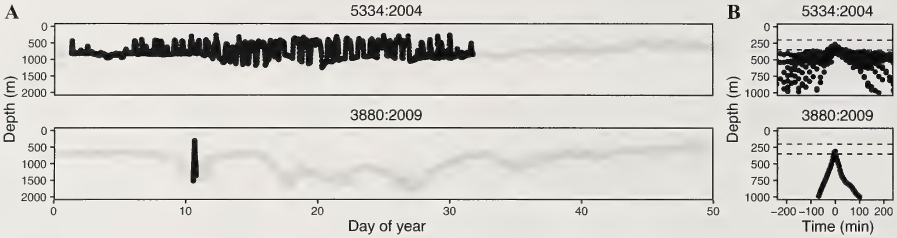

Figure 6

Putative *spawning rises*, meaning abrupt movements of fish to shallower depths, identified in archival tag data for 2 Greenland halibut (*Reinhardtius hippoglossoides*) of undetermined sex tagged in 2004 (tag no. 3880) in the eastern Bering Sea and in 2009 (tag no. 5334) in the Aleutian Islands. (**A**) Tag-recorded depths of fish are provided for the first 50 d of the year (grey circles), with black circles indicating depths during spawning rises. Panel titles are the tag number and the year data were recorded (e.g., *5334:2004* means data recorded in 2004 for the fish implanted with tag no. 5334). (**B**) Close-ups of spawning rises that reached a depth <400 m are provided, with the time for the minimum depth recorded set to 0 min to align all the rises. In each B panel, horizontal dashed lines at depths of 200 and 350 m are shown as references.

that males have a prolonged spawning state during which their vertical activity increases. The single spawning rise means that females spawn once in a year and do not hydrate multiple batches of eggs, and this finding supports the results of recent studies that indicate that 2 cohorts of vitellogenic oocytes are not spawned in the same season (Kennedy et al., 2011). In a study of gonad development of Greenland halibut in the Barents and Norwegian Seas, males spawned over an extended period and females had a bimodal split between prespawning and postspawning (Albert et al.[2]). The results of that study are consistent with our finding that males actively spawn for a protracted period and females actively spawn for a very narrow period. Sex-specific differences that have been identified for Pacific and Atlantic halibut are nearly identical to observations for Greenland halibut, with males having more sporadic and protracted spawning behavior relative to the abrupt rises of females (Loher and Seitz, 2008; Murphy et al., 2017). The increase in vertical movements of male Greenland halibut during this presumed spawning time identified in these studies and in our study contrasts with reported spawning activity of Atlantic cod (*Gadus morhua*): a tide is evident in depth profiles of males that sit in lekking arenas waiting for females to spawn (e.g., Meager et al., 2010).

These differences could also be used to infer sex for tagged Greenland halibut that did not have their sex determined but were at liberty through the winter. For example, one fish of undetermined sex had spawning activity with the expected prolonged, regular periodicity of typical male behavior, and another fish that did not have its sex determined had the isolated spawning rise of a female (Fig. 6). Previous research in which archival tags were used on Greenland halibut (e.g., Peklova et al., 2012) should be reexamined for evidence of these behaviors and their annual consistency, given that this study was focused on the BSAI region and that our results cannot be applied to all populations across the range of this species. Boje et al. (2014) made at least one reference to a Greenland halibut suddenly ascending from a depth of approximately 800 m up to a depth of 450 m within 1 h during November, a movement that appears similar to the presumed spawning rises we have described. Identification of the presence or absence of this singular annual spawning rise for female Greenland halibut in other regions would be informative.

The likelihood of a female Greenland halibut exhibiting spawning behavior may be delineated by length. The 2 females that did not have spawning rises were the smallest females recovered, at 68 and 71 cm FL, and the 3 females that did exhibit this spawning behavior were larger than 83 cm FL. We hypothesize that these smaller fish did not have spawning rises because they were not yet mature. It is possible that they did spawn without an obvious ascent like the larger fish, and additional research, such as deployment of the SeaTag-SP (Desert Star Systems, LLC, Monterey Bay, CA), which transmits a location and archival data when spawning occurs, could help clarify whether such small females are spawning with or without rises. Alternatively, a lack of spawning rises detected in archival tag data for the small Greenland halibut may not be associated with size and could be indicative of skipped spawning. Skipped spawning, when a mature fish does not spawn, occurs in many taxa, such as the Pacific halibut (Loher and Seitz, 2008), sablefish (*Anoplopoma fimbria*) (Rodgveller et al., 2016), and *Sebastes* species (Conrath, 2017). Skipped spawning has been suggested for Greenland halibut (Fedorov, 1971); however, this behavior seems an unlikely explanation because it would mean that these small fish were already mature at an even smaller size. Given the more recent interpretation of gonad development of female Greenland halibut and the lack of spawning evidence for small females, the L_{50} currently used in stock assessments may be an underestimate, and the maturity classifications for Greenland halibut in the BSAI region should therefore be revisited.

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[2] Albert, O. T., E. M. Nilssen, A. Stene, A. C. Gundersen, and K. H. Nedreaas. 1998. Spawning of the Barents Sea/Norwegian Sea Greenland halibut (*Reinhardtius hippoglossoides*). ICES CM Doc. 1998/O:22, 19 p. [Available from website.]

Tagging research focused on spawning behavior should consider several aspects of study design. When archival tags have a temporal data resolution that is too coarse (e.g., hourly), they are unlikely to capture behaviors of short durations such as spawning (Fisher et al., 2017). Tag sampling intervals must be set appropriately to capture the behavior of interest. For spawning of large flatfish, 1-min intervals are appropriate, but if multiyear data are desirable, a longer interval may be necessary to extend battery life. Type of tag is another consideration; pop-off satellite archival tags are often chosen because fish do not need to be recaptured to retrieve data, whereas the use of archival tags that had to be implanted in fish in this study required a large number of tags to be deployed relative to the number of tags recovered with usable data. A drawback in several studies of spawning in which pop-off satellite archival tags were used is the lack of sex information associated with the tag data retrieved (unless the fish is recaptured and visually inspected); this issue could be remedied through genetic sampling at the time of release (e.g., Goetz et al., 2018). Tags that provide data that can be used to confirm these presumed behaviors are becoming available. The previously mentioned SeaTag-SP could be used to corroborate the assumption that spawning has occurred and to aid estimation of the location and timing of spawning.

Conclusions

Tagging studies can be used to generate and test hypotheses related to fish behavior; for example, analysis of tag data can determine spawning timing and location. Tag data also can be used in concert with data from other sources to provide a more complete view of the life history for large species that are difficult to sample. The findings from our analysis of data from tags implanted in Greenland halibut in the BSAI region are as follows: 1) spawning occurs in January and February; 2) eggs are released at depths of 200–350 m below the surface; 3) females are total spawners, releasing eggs only once during a year; and 4) a female can spawn in consecutive years. Data from deployment of additional tags could also support a revised L_{50} for Greenland halibut based upon dimorphic rising behavior or could also be used to infer a minimum size at spawning, information that could aid in defining lengths in maturity tables. The use of archival tags should therefore be considered as a complement (when appropriate) to other methods when designing future research on fish behavior.

Acknowledgments

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Overwinter habitat use of young-of-the-year white sharks (*Carcharodon carcharias*) off the eastern United States

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Abstract—Despite recent increases in the number of studies that have focused on the movements and habitat use of juvenile and adult white sharks (*Carcharodon carcharias*) in the Northwest Atlantic Ocean off the eastern United States, there is comparatively little information on the movements of young-of-the-year (YOY) white sharks, particularly in the overwinter season. Simultaneous satellite and acoustic tagging were conducted on YOY white sharks in 2016 and 2017, and data from their first overwinter period (December through April) were analyzed. Tracks of 9 white sharks offer a preliminary characterization of overwinter habitat use. During 2 winter periods over consecutive years, YOY white sharks occupied continental shelf waters (bottom depths: <100 m) off the coasts of North and South Carolina with mean sea-surface temperatures of 14.9–21.2°C, mean sea-surface heights of −0.5–0.2 m, and mean chlorophyll-*a* concentrations of 0.4–2.8 mg/m^3. Their overwinter habitat extended over 950 km south of the current essential fish habitat established for YOY white sharks; however, it did overlap with a seasonal closure area that restricts bottom longline fishing. These results provide preliminary evidence for the existence of an overwinter nursery area for YOY white sharks in U.S. waters of the Atlantic Ocean.

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Effective conservation and management of highly migratory marine species relies on adequate characterization of focal habitat areas that often vary across seasons (Federal Register, 2017; Kohler and Turner, 2019). The designation of essential fish habitat (EFH) for every fish stock federally managed under the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens . . . 2020) provides a platform for managers to analyze and mitigate the effects on those habitats from fisheries, coastal development, and offshore energy activities (Federal Register, 2017). However, fundamental data on distribution and habitat association are lacking for many highly migratory species. This lack of information is particularly true for the young-of-the-year (YOY) and juvenile life stages of many shark species found in U.S. waters of the Atlantic Ocean, given that most habitat use studies have focused on nursery areas used in summer, when species are abundant in nearshore or inshore areas that can be easily sampled (Heupel et al., 2007; McCandless et al., 2007). There has been considerably less research on overwinter habitats of juvenile sharks, owing to the logistical difficulties of field sampling during winter months in northern latitudes.

Research into the seasonal movements and habitat of YOY white sharks (*Carcharodon carcharias*) in the Northwest Atlantic Ocean has only recently advanced, facilitated by multiple electronic tagging and tracking studies (Curtis et al., 2018; Shaw et al., 2021). Although Casey and Pratt (1985) were the first to report the occurrence of YOY and juvenile white sharks in the New York Bight, Curtis et al. (2018)

confirmed that this region functions as a summer nursery area, using satellite and acoustic telemetry. During this season, YOY white sharks typically occupy waters off the south shore of Long Island, New York, in depths <40 m, sea-surface temperatures (SST) of 18–22°C, and chlorophyll-*a* (Chl-*a*) concentrations >2 mg/m^3 (Shaw et al., 2021). Despite this improved understanding of the summertime habitat use of YOY white sharks, information on overwinter habitat use has been limited to data for only a few individuals tracked to coastal waters of North and South Carolina from December 2016 through April 2017 (Curtis et al., 2018). Larger juvenile and adult white sharks (>2.5 m in total length [TL]) typically overwinter over a broad area encompassing the east and west coasts of Florida and occasionally offshore pelagic waters (Adams et al., 1994; Curtis et al., 2014; Skomal et al., 2017), but it is not known if YOY white sharks occupy similar areas during this season.

In U.S. waters of the Atlantic Ocean, the white shark is a prohibited species under National Marine Fisheries Service (NMFS) Atlantic Highly Migratory Species fishery regulations. The NMFS also designates EFH for YOY, juvenile, and adult white sharks to help minimize adverse effects on habitats important to each of these life stages, with the current EFH for YOY white sharks covering a broad portion of the continental shelf waters from Cape Cod, Massachusetts, to southern New Jersey (Federal Register, 2017). Although not specifically designed to protect white sharks, several fishery time-area closures in the U.S. waters of the Atlantic Ocean afford protections to coastal and pelagic shark populations (NMFS[1]). Relative abundance of white sharks in the Northwest Atlantic Ocean appears to be increasing in response to these fisheries management measures; however, the population remains data poor and biologically vulnerable, and there is uncertainty in regional population dynamics (Curtis et al., 2014; Skomal et al., 2017).

The purposes of this study were to provide the first characterization of overwinter distribution and habitat use of YOY white sharks and to assess the degree to which existing spatial fisheries management measures align with that distribution. The results of this work enhance the growing body of information on the spatial ecology of white sharks in the Northwest Atlantic Ocean off the eastern United States (Curtis et al., 2014; Skomal et al., 2017; Curtis et al., 2018; Shaw et al., 2021) and provide data necessary for making practical recommendations that may improve fisheries management.

Materials and methods

Young-of-the-year white sharks were tagged during August in 2016 and 2017 by using methods described by Curtis et al. (2018) and Shaw et al. (2021). Briefly, recreational rod-and-reel shark fishing techniques were used to catch sharks offshore of Montauk, New York. Upon capture, each shark was guided to a boatlift platform on the MV *OCEARCH* and raised out of the water for tagging and sample collection, while a raw seawater hose was placed in its mouth to irrigate its gills. A satellite-linked smart position or temperature transmitter (SPOT-258A[2], Wildlife Computers Inc., Redmond, WA; 3-year tag life) and an acoustic transmitter (Vemco V16-6H, Innovasea Systems Inc., Boston, MA; 10-year tag life) were attached to each shark. Smart position or temperature tags were attached to the first dorsal fin, permitting tag transmission to Argos satellites whenever the fin broke the sea surface. Acoustic transmitters were surgically implanted into each shark's coelomic cavity through a small incision that was sutured closed. Handling and tagging of all sharks was done in compliance with all applicable guidelines and regulations, and the research was conducted under permits from the NMFS and the New York State Department of Environmental Conservation.

The overwinter period was defined as that from December through April on the basis of previous data (Curtis et al., 2018), and only tag detections from that period were analyzed. Acoustic detections were received from moored acoustic receivers (Vemco VR2W, Innovasea Systems Inc.) maintained by cooperating members of the Mid-Atlantic Acoustic Telemetry Observation System (MATOS) along the East Coast of the United States (e.g., Bangley et al., 2020a). Positions transmitted to Argos satellites with location quality classes of 0–3, A, and B (i.e., the highest quality locations, with estimated errors less than approximately 15 km) were chronologically combined with passive acoustic detections of tags received from the MATOS network to produce positions for each shark, following Shaw et al. (2021). Erroneous points, including points on land, and points with an Argos location quality worse than B were removed from the analysis. One unique tag transmission per shark per day was selected on the basis of location quality, and daily positions were made regular by interpolating positions to fill gaps up to 7 d between consecutive tag detections with the ArcMET extension for ArcGIS 10.3 (Esri, Redlands, CA) (Curtis et al., 2018; Shaw et al., 2021). No positions were interpolated for tag detection gaps greater than 7 d in duration.

Four environmental variables were used to characterize habitat use: SST, Chl-*a* concentration, sea-surface height (SSH), and bathymetry. Underlying depths were derived from the NOAA ETOPO1 Global Relief Model, a data set of land topography and ocean bathymetry with a 1-arcmin resolution (NOAA National Geophysical Data Center, available from website), and each depth was matched to a raw coordinate position in ArcGIS. Group for High Resolution SST Level 4 data from the Jet Propulsion Laboratory were compiled at a spatial resolution of 0.01° (available from website). Weekly Chl-*a* concentrations were compiled from data from the NOAA Visible Infrared Imaging Radiometer Suite at a spatial resolution of 4.17 km (available from website). Daily SSH data were collected from the Naval Oceanographic Office Hybrid Coordinate Ocean Model and Navy Coupled Ocean Data Assimilation at a spatial resolution of 1/12° (available from website). Values for oceanographic characteristics were matched to daily shark positions by using the xtractomatic function in R, vers. 3.6.0 (R Core Team, 2019).

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[1] NMFS (National Marine Fisheries Service). 2019. Issues and options for research and data collection in closed and gear restricted areas in support of spatial fisheries management, 27 p. Natl. Mar. Fish. Serv., Silver Spring, MD. [Available from website.]

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

All location and environmental data were visualized by using ArcMap 10.7 (Esri). The overwinter cumulative activity space (i.e., home range) for the tracked sharks was characterized by using a minimum convex polygon. By using ArcMap, the resulting minimum convex polygon was compared to spatial management areas for highly migratory species, including to the boundaries of the current EFH for YOY white sharks (Federal Register, 2017) and to the Mid-Atlantic Shark Closure Area—an area off North Carolina that is closed to shark bottom longline fishing from 1 January through 31 July each year to reduce fishing mortality on overfished dusky (*Carcharhinus obscurus*) and sandbar (*C. plumbeus*) sharks (NMFS[1]).

Results

Twenty YOY white sharks were tagged near Montauk, New York, in August 2016 (number of samples [*n*]=9) and August 2017 (*n*=11). For 9 of those sharks, 1111 tag detections were recorded in their first overwinter period (2016: *n*=4; 2017: *n*=5) (Table 1). Analysis of habitat use was based on a total of 184 daily positions, including 19 detections from 16 acoustic receivers at unique locations in the MATOS network, 76 positions transmitted to Argos satellites, and 89 positions interpolated between tag detections. During both years, sharks occupied a similar distribution, mostly in continental shelf waters off the coasts of North and South Carolina (32–37°N) (Fig. 1A). The sharks traveled along the coastline mostly over depths <100 m, although a few excursions were made beyond the continental shelf break over bottom depths >2000 m. The mean depth associated with tag positions was 74 m (standard deviation [SD] 329) when these extreme depths are included. However, 92% of all positions occurred over depths <80 m.

The YOY white sharks were exposed to similar ranges of oceanographic conditions in their overwinter habitat. The SSTs ranged from 12.9°C to 23.4°C with a mean of 18.4°C (SD 2.5). The majority of observations (60%) fell within a range of 16.0–21.0°C. Despite their proximity to the Gulf Stream, the tagged sharks generally were not located in its warmer waters (Fig. 1A). The YOY sharks occurred in waters with a mean SSH of −0.5 m (SD 0.2) and rarely occurred in areas with positive SSH (e.g., the Gulf Stream) or in areas with SSH less than −0.9 m. Additionally, the sharks used somewhat productive areas with

Table 1

Descriptions of 9 young-of-the-year white sharks (*Carcharodon carcharias*) tracked in the Northwest Atlantic Ocean during winter months (December–April) between 2016 and 2018, as well as of their tracking and detected positions and of characteristics of the habitat they used. Mean and range of sea-surface temperature (SST), depth (bathymetry), chlorophyll-*a* (Chl-*a*) concentration, and sea-surface height (SSH) are provided with standard deviations in parentheses. Shark IDs correspond to the individual sharks described in Shaw et al. (2021).

Shark ID	Total length (cm)	Sex	Tracking period	No. daily positions	SST (°C)	Depth (m)	Chl-*a* (mg/m^3)	SSH (m)
WS1	142	F	8-Dec-2016 to 29-Jan-2017	13	15.3 (0.9)	90 (89)	0.7 (0.6)	−0.6 (0.1)
					14–16.5	14–339	0.3–2.3	−0.7–0.5
WS2	158	M	17-Jan-2017	1	20.4	27	1.0	−0.6
					–	–	–	–
WS7	162	F	10-Mar-2017	1	17.9	39	1.2	−0.7
					–	–	–	–
WS8	162	M	4-Dec-2016 to 20-Apr-2017	17	18.6 (2.0)	30 (5.5)	1.3 (0.7)	−0.6 (0.1)
					13.5–21.7	18–41	0.6–3.2	−0.9–0.4
WS9	150	M	22-Dec-2017 to 5-Mar-2018	43	19.5 (2)	45 (57)	0.7 (0.6)	−0.5 (0.1)
					14.6–22.8	7–342	0.3–3.2	−0.9–0.2
WS11	166	M	5-Dec-2017 to 8-Mar-2018	70	18.6 (2.3)	124 (527)	0.8 (0.9)	−0.5 (0.2)
					12.9–23.4	1–3283	0.2–6.1	−0.8–0.1
WS13	147	M	2-Dec-2017 to 2-Apr-2018	16	14.9 (1.3)	13 (4)	1.8 (0.6)	−0.4 (0.2)
					13.5–17.1	6–20	0.8–2.7	−1.0–0.1
WS16	154	F	5-Dec-2017 to 1-Apr-2018	8	16.4 (1.0)	9 (5)	2.8 (1.3)	−0.4 (0.2)
					15.5–17.8	5–14	1.4–4.0	−0.7–0.1
WS17	152	F	2-Feb-2018 to 16-Feb-2018	15	21.2 (0.6)	57 (30)	0.4 (0.1)	−0.6 (0.1)
					19.4–22.0	27–134	0.3–0.7	−0.7–0.5

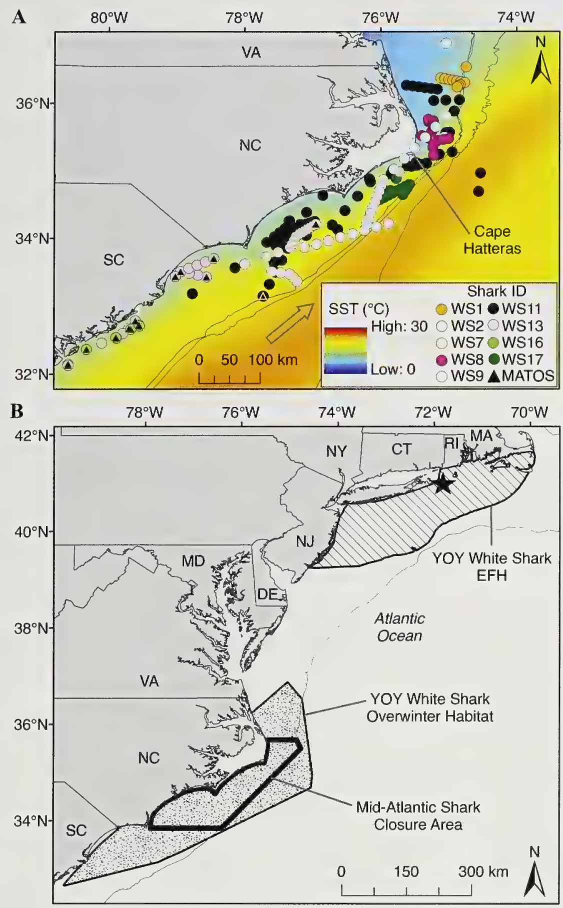

Figure 1

Maps showing (**A**) daily positions (colored circles) and (**B**) the minimum convex polygon that delineates the area of cumulative activity space (i.e., home range; stippled area) based on detections of tags attached to or implanted in 9 young-of-the-year (YOY) white sharks (*Carcharodon carcharias*) tracked off the East Coast of the United States from December through April during 2016–2018. In panel A, positions are shown over average winter sea-surface temperatures (SST) and the 100-m, 200-m, and 2000-m isobaths (gray lines). Triangles indicate the locations of acoustic receivers in the Mid-Atlantic Acoustic Telemetry Observation System (MATOS), and the open arrow denotes the location and direction of the Gulf Stream. Shark IDs correspond to individual sharks described in Shaw et al. (2021). In panel B, the area of cumulative activity space of tracked sharks is compared to the 200-m isobath (gray line), to the current essential fish habitat (EFH) area designated by the National Marine Fisheries Service for YOY white sharks (hatched area), and to the Mid-Atlantic Shark Closure Area (polygon outlined with a thick black line). The black star in the EFH denotes the location where sharks were tagged in August 2016 and 2017.

Chl-*a* concentrations of 0.2–6.1 mg/m^3 (mean: 1.0 mg/m^3 [SD 0.9]).

Overwinter distribution relative to key fisheries management boundaries varied. Positions of YOY white sharks did not overlap at all with the current EFH designated for this life stage, and they actually extended up to 960 km beyond the current EFH boundary (Fig. 1B). In contrast, the overwinter distribution of YOY white sharks significantly overlapped with the Mid-Atlantic Shark Closure Area. Over half (54%) of the daily positions indicate that tagged sharks were within the boundaries of the closure area during the time the closure was in effect (from 1 January through July 31).

Discussion

The results of this study improve the understanding of overwinter distribution and habitat use of YOY white sharks in the Northwest Atlantic Ocean, and this advancement is important because YOY is a life stage that has been historically little studied in this region (Curtis et al., 2018; Shaw et al., 2021). Preliminarily, results from analysis of tracking data for 9 individuals from 2 cohorts indicate that YOY white sharks make seasonal migrations to the coastal waters of North and South Carolina during their first winter period (from December through April). The combination of both satellite and acoustic tag technologies provided more insight into overwinter habitat use than either technology would have on its own, as has been recently reported for habitat use of YOY white sharks in their summer nursery area in the New York Bight (Curtis et al., 2018; Shaw et al., 2021).

The data presented herein support the hypothesis that the area occupied by these tracked YOY white sharks represents an overwinter nursery area. The area meets the shark nursery area criteria proposed by Heupel et al. (2007): our data indicate that YOY white sharks occur more frequently in this area than in other areas during winter (criterion 1), they remain in the area for an extended period (criterion 2), and they use the same area repeatedly across years (criterion 3). However, this information is based on only the movements of 9 individuals across 2 years, and

2 individuals were detected only on a single day. Unlike that for the summer nursery area used by white sharks in the New York Bight, the historical data that support any of the nursery area criteria for the habitat used in winter is minimal (Casey and Pratt, 1985; Castro, 2011; Curtis et al., 2014, 2018). Additional research is needed to more fully address whether coastal waters of North and South Carolina include overwinter nursery habitat for YOY white sharks, although the region appears to contain similar habitats and environmental conditions selected by YOY and juvenile white sharks in other regions (Weng et al., 2007; Bruce et al., 2019; White et al., 2019; Shaw et al., 2021).

There was some overlap, but YOY white sharks occurred in geographic areas different from those where larger juveniles (>2.5 m TL) and adults occurred during winter months (Curtis et al., 2014; Skomal et al., 2017; Curtis et al., 2018). Specifically, larger white sharks typically move through North and South Carolina as they migrate south during fall and winter, and they generally overwinter off the Atlantic and Gulf coasts of Florida (Casey and Pratt, 1985; Adams et al., 1994; Castro, 2011; Curtis et al., 2014; Skomal et al., 2017). Despite acoustic receiver coverage south of the area occupied by the tagged individuals (Bangley et al., 2020a), YOY white sharks did not appear to migrate as far south as most larger white sharks (Skomal et al., 2017), thereby maintaining a level of size-based spatial segregation in the population. Although this segregation may be the result of smaller body sizes and the related physiological constraints to migration for YOY white sharks, it could also reflect local resource availability or an evolutionary adaptation that reduces predation risk. Larger white sharks, dusky sharks, tiger sharks (*Galeocerdo cuvier*), and bull sharks (*Carcharhinus leucas*) are the most likely predators of YOY white sharks in this region. Numerous shark species seasonally co-occur with YOY white sharks, but such large predators appear to be uncommon in waters of North and South Carolina during the winter (Lea et al., 2015; Skomal et al., 2017; Calich et al., 2018; Kohler and Turner, 2019; Bangley et al., 2020b; Logan et al., 2020). The reduced predation pressure from the segregation of life stages of white sharks provides further support for the notion that this region may serve as a nursery through enhanced survival of young white sharks (Heupel et al., 2007).

Fisheries and environmental resource managers can use the increased understanding of seasonal distribution from this study to improve conservation of YOY white sharks and to evaluate the effects of human activities on their overwinter habitat. Although the current EFH for YOY white sharks does not encompass the overwinter habitat areas identified in this study, it was established by using observations compiled prior to any significant electronic tagging and tracking research on this life stage of this species (Federal Register, 2017). Our results may inform future reviews and updates to EFH by the NMFS and may allow improved mitigation of anthropogenic effects on these important habitats by state and federal agencies. Already, YOY white sharks appear to benefit incidentally from the current Mid-Atlantic Shark Closure Area, which minimizes bottom longline fishery bycatch during the period YOY white sharks occur in that area. Telemetry has revealed that other regional shark species also benefit from this time-area closure, providing empirical evidence that could be used to improve the timing and location of such areas (Calich et al., 2018; Bangley et al., 2020b; Logan et al., 2020). In this case, hypothetically shifting the closure period to start and end one month earlier (i.e., to occur from 1 December through 30 June) would increase overlap of the closure with YOY white sharks by an additional 6%. Additional research will help further refine spatial management and estimate bycatch susceptibility of white sharks across seasonal habitats.

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First observation of the use of coral habitat by larval northern rockfish (*Sebastes polyspinis*) in the western Gulf of Alaska

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Abstract—The role of deepwater corals and sponges in the life history of fish species is generally unknown for the larval stage. In 2017, we deployed an autonomous plankton pump into deepwater coral habitat (depths: >50 m) to examine which species were present and captured a single rockfish larva. Using genetic methods, we identified the larva as a northern rockfish (*Sebastes polyspinis*). The unique capture of a free-swimming larva with a plankton pump in this study is the first in situ record of the use of deepwater coral habitat by rockfish larvae. Subsequent reexamination of coral specimens captured in bottom-trawl surveys that had been conducted in the Gulf of Alaska yielded an additional 10 northern rockfish larvae and a single harlequin rockfish (*S. variegatus*) larva lodged in the polyps of 2 species of deepwater coral. The results of this study improve our knowledge of the early life history of rockfish species, a taxonomic group that has limited lifetime dispersal indicated by a high degree of population structure. The capture and identification of the larva also indicate a potential mechanism for larval retention in the area of their extrusion and highlight the further importance of deepwater coral habitat as essential habitat for rockfish species.

Deepwater coral and sponge habitats have been reported to support a higher diversity and abundance of many marine fish and invertebrate species than other non-structured habitats (Buhl-Mortensen and Mortensen, 2004; Watling et al., 2011). In the Northeast Pacific Ocean, rockfishes (*Sebastes* spp.) are linked to deepwater (depths: >50 m) corals and sponges because of their preference for structured habitats (Rooper et al., 2007). These studies were conducted almost exclusively on the juvenile and adult stages of the life history of rockfishes and other species, and the role of deep-sea corals and sponges in the larval stage of rockfishes is unknown. Understanding whether rockfish in early life stages utilize deep-sea coral and sponge habitats as settlement or nursery grounds is key to understanding their full life history and to conserving essential habitat.

Early juvenile stages of rockfishes have been found to recruit in higher densities to structured habitats than in habitats without structure (Love et al., 1991; Rooper et al., 2007; Love et al., 2012), indicating that structured habitats are used as nurseries by rockfish in early life history stages. It has been observed that, in shallow coral reef habitats (depths: <50 m), larval fish migrate vertically downward into corals to avoid currents, movements that can prevent larvae from being carried away and, therefore, can help them remain in coral habitat (Paris and Cowen, 2004). Redfish larvae (*Sebastes* spp.) have been captured in close association with sea pens (order Pennatulacea) by using bottom-trawl gear (Baillon et al., 2012). Sea pens may serve a similar purpose as corals in shallow-water habitats, by retaining larvae in nursery habitats with seafloor structure. These observations have led to the hypothesis that rockfish in early life history stages recruit to and are retained in deep-sea coral habitats that are beneficial to their

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survival. Several factors have led to difficulty in exploring this hypothesis. First, trawling for samples both destroys the habitat (Hourigan, 2009; Clark et al., 2016) and integrates catches over large distances, making fine-scale associations difficult to determine. Second, identification of the early life stages of rockfishes is difficult prior to development of distinguishing characteristics (Matarese et al., 1989; Johansson et al., 2018).

We developed a plankton pump to sample zooplankton and larval fish in deepwater coral habitat in Alaska (Wilborn et al., 2020). The plankton pump provides a non-destructive method of sampling that can provide fine-scale information on habitat associations. The aim of this study was to explore the potential role of deep-sea coral habitat in the early life history of rockfishes in the North Pacific Ocean without damaging the habitat. Genetic techniques solved the second issue of species identification. The objectives of this note are to report the first known instance of a single larval rockfish captured directly from deep-sea coral habitat and to discuss supplementary evidence from larval rockfish captured in association with deep-sea corals during bottom-trawl surveys in the Gulf of Alaska.

Materials and methods

The method used to capture zooplankton and larval fish from coral and sponge habitats in the Gulf of Alaska is described in Wilborn et al. (2020). In brief, the plankton pump is an autonomous sampler that was deployed from a contracted research vessel at depths of 80–105 m. We deployed the pump 8 times, in areas of known coral and sponge habitat, as well as in areas without coral and sponge habitat (5 and 3 deployments, respectively). It was programmed to sample the seafloor plankton by drawing water through a 333-µm-mesh zooplankton net. Sampling began after the pump reached the seafloor and ended after 15 min, with an automated door closure preventing contamination of the sample during retrieval. The mean volume of water filtered per deployment was 6.32 m^3 (standard deviation 2.46). Prior to retrieval of the plankton pump, a series of photographs of the seafloor were taken by a camera mounted on the pump to document the surrounding habitat. The 8 samples were collected in the western Gulf of Alaska between the Shumagin Islands (~158°W) and Samalga Pass (~170°W) in 2017 (further details on this sampling and the organisms captured can be found in Wilborn et al., 2020). All samples collected from the plankton pump were individually extracted and preserved in plastic containers with a 95% solution of ethanol and glycerol for further analysis in the laboratory.

To genetically identify the larval rockfish captured in the plankton pump, a 750-base-pair (bp) region of the mitochondrial cytochrome *b* gene was amplified to identify the rockfish to species. This method has been used successfully to discriminate among known species of rockfish (Rocha-Olivares et al., 1999). For each sampled larva, DNA was extracted from the caudal fin by using a QIAamp[1] DNA micro kit (Qiagen Inc., Hilden, Germany) and eluted in 25 µL of buffer. The mitochondrial DNA fragment of the cytochrome *b* gene was amplified through a polymerase chain reaction cocktail by using primers GluDG (5' TGA CTT GAA RAA CCA YCG TTG 3') and CB3R (5' ATA TCA TTC TGG CTT AAT GTG 3') as described in Rocha-Olivares et al. (1999). Thermalcycling conditions were 90°C for 2 min, followed by 36 cycles of 94°C for 50 s, 51°C for 50 s, and 72°C for 50 s. Polymerase chain reaction fragments were visualized with E-Gel EX Agarose gels (1%; Thermo Fisher Scientific, Waltham, MA). Polymerase chain reaction products were cleaned and sequenced in forward and reverse directions at Molecular Cloning Laboratories in San Francisco, California. The resulting data were assembled in Sequencher, vers. 5.0 (Gene Codes Corp., Ann Arbor, MI). High-quality forward and reverse sequences (with quality scores >40) were aligned to produce a 655-bp fragment of the mitochondrial cytochrome *b* region in Sequencher. Consensus sequences were aligned in the sequence alignment editor in BioEdit (vers. 7.2; Hall, 1999) to highlight differences, and trimmed sequences were assigned GenBank accession numbers (Table 1) (GenBank, available from website).

In addition to analyzing DNA from the single unknown rockfish larva, for comparison, we sequenced DNA from adults of 4 species of rockfish known to occur in the region where the larva was collected (Table 1). The new sequences of DNA from these adults were cataloged in the University of Washington Fish Collection (available from website). The 4 species are Pacific ocean perch (*Sebastes alutus*) (voucher no. UW151031), dusky rockfish (*S. ciliatus*) (UW155786), northern rockfish (*S. polyspinis*) (UW155787 and UW189442), and light dusky rockfish (*S. variabilis*) (UW45510). We also compared the DNA from the larva to DNA from another available specimen of northern rockfish (UW113251) for which DNA had been sequenced during an unrelated study in the eastern North Pacific Ocean (at 52°34′N, 170°41′W) in 2004. We expected the unknown rockfish larva to be identified either through sequences from the 6 samples on hand or through sequences available in open-access repositories of genetic data (e.g., GenBank).

Subsequent to the capture of the northern rockfish larva in 2017, a reexamination of corals collected during the bottom-trawl survey conducted by the NOAA Alaska Fisheries Science Center in the Gulf of Alaska in 2017 was undertaken. These coral specimens were collected as part of routine efforts to collect genetic information on corals and sponges in the Gulf of Alaska. Additional rockfish larvae were found lodged in specimens of 2 species of coral (a *Plumarella superba* and a *Callogorgia compressa*; Fig. 1). The larvae and corals were collected on 30 May 2017 from the haul of a bottom-trawl tow conducted at a depth of 136 m in the Gulf of Alaska (52°41′N, 169°32′W). The DNA from 5 individuals associated with *Callogorgia compressa* and from 6 individuals associated with

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[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

GenBank accession numbers, corresponding University of Washington Fish Collection database (UW) voucher numbers, and species names of individual rockfish (*Sebastes* spp.) that had their DNA sequenced for comparison to DNA from the larval rockfish collected as part of this study in 2017 in the Gulf of Alaska. GenBank accession numbers for an additional 11 larvae were OM141006–OM141016.

UW voucher no.	Species identified	Species common name	GenBank no.
UW155787	*S. polyspinis*	Northern rockfish	MH686385
UW45510	*S. variabilis*	Light dusky rockfish	MH686386
UW151031	*S. alutus*	Pacific ocean perch	MH686387
UW155786	*S. ciliatus*	Dusky rockfish	MH686388
UW189442	*S. polyspinis*	Northern rockfish	MH686389

Plumarella superba were sequenced by using the same methods described in a previous paragraph. Species identification was performed by comparing the resulting sequences to sequences from this study (Table 1) or to sequences found in GenBank by using the Basic Local Alignment Search Tool (BLAST, available from website) (Johnson et al., 2008) if an exact match did not exist among sequences provided in Table 1.

Results and discussion

A sample collected with the plankton pump on 8 June 2017 in the Gulf of Alaska south of Unimak Island, Alaska (54°10′N, 162°14′W), at a depth of 93 m in coral habitat included a single larval rockfish (Fig. 1). No larvae were captured in samples taken during the other 7 deployments of the plankton pump. The habitat where the larval rockfish

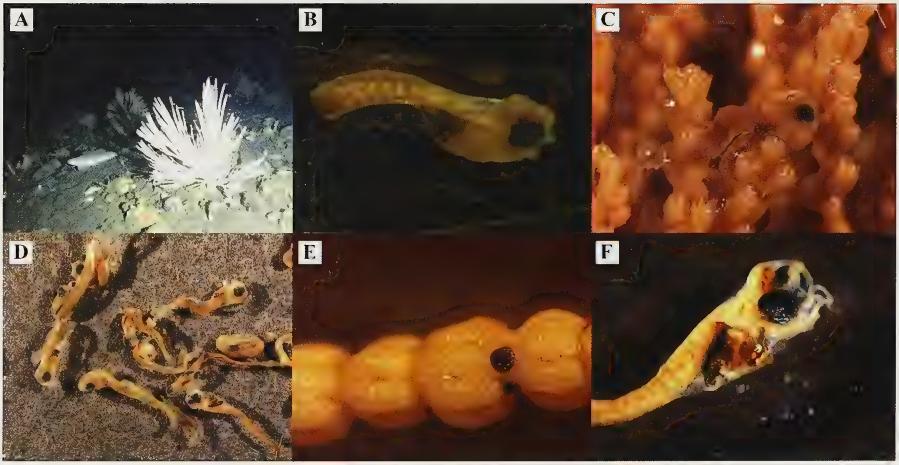

Figure 1

Images of deepwater coral habitat and rockfish larvae (*Sebastes* spp.) associated with collections made with a plankton pump during this study or made during the bottom-trawl survey conducted by the NOAA Alaska Fisheries Science Center (AFSC) in the Gulf of Alaska in 2017: (**A**) deepwater coral habitat where the larval northern rockfish was collected with the plankton pump, (**B**) the northern rockfish larva collected in the plankton pump, (**C**) a larval rockfish with a coral of *Plumarella superba* from the collection of specimens captured during the AFSC bottom-trawl survey, (**D**) rockfish larvae collected from corals sampled during the AFSC bottom-trawl survey, (**E**) a larval rockfish nestled in a coral of *Callogorgia compressa* collected during the AFSC bottom-trawl survey, and (**F**) a larval rockfish retrieved from the collection of the AFSC bottom-trawl survey.

was captured was predominantly soft sediment but had some cobble and boulder-sized rocks intermixed throughout. Corals (especially *Callogorgia* sp.) were abundant at the deployment location where the larva was captured and on the surrounding seafloor (Fig. 1). The specimen was 5.53 mm in length and weighed 0.2 g. The size of extrusion for northern rockfish is not known but is expected to be less than 6.1 mm (Matarese et al., 1989), and in general the size of extrusion for most rockfish species is 5–7 mm (Love et al., 2002). The specimen was visually identified as a rockfish (*Sebastes* sp.) and was considered to have recently extruded because of its small size.

The larval specimen in question differed by 1 bp at position 246 from the vouchered northern rockfish specimen (UW155787) but was an exact match to the our newly sequenced northern rockfish specimen (UW189442) and to 2 specimens of northern rockfish in GenBank: catalog no. EF446443.1 (voucher no. UW113251) and catalog no. DQ678512.1 (voucher no. SQFSC121-69 (Hyde and Vetter, 2007). Therefore, we concluded that this larval fish was a northern rockfish.

For the additional 11 larvae associated with corals, all sequences associated with *Plumarella superba* and 4 of the 5 larvae associated with *Callogorgia compressa* matched the sequence for our recent specimen (UW189442) (Table 1) and were identified as northern rockfish. One individual associated with *Callogorgia compressa* matched the sequence for DQ678476.1 (SWFSC173-8) and was identified as a harlequin rockfish (*S. variegatus*) (Hyde and Vetter, 2007). These 11 larvae were all found in corals, settled among polyps as shown in Figure 1. This observation is similar to that of Baillon et al. (2012), who also observed larvae of Atlantic redfish (*Sebastes* sp.) situated among polyps of pennatulaceans in trawl hauls. Baillon et al. (2012) observed the Atlantic redfish larvae in bottom-trawl hauls that also captured adult Atlantic redfish; therefore, the larvae may have been extruded in the net and swept into the pennatulacean polyps by the action of the trawl gear. During the bottom-trawl survey conducted in 2017 in the Gulf of Alaska, adult northern rockfish did occur in 1 of the 2 trawl hauls in which its larvae were also captured, but adult harlequin rockfish did not occur in the bottom-trawl haul in which the larval harlequin rockfish was found, indicating that the occurrence of these larvae on corals was not necessarily a consequence of the capture process inducing extrusion of rockfish larvae within the trawl net.

The capture of free-swimming northern rockfish larvae by using a plankton pump is the first in situ record of a rockfish larva confirmed to have been captured from within deepwater coral habitat. Little is known of the early life history of Alaska rockfishes or of northern rockfish in particular, but species of *Sebastes* generally have an extensive pelagic larval phase of up to 1 year in duration and a limited lifetime dispersal indicated by genetic studies (Miller and Shanks, 2004; Hyde and Vetter, 2007; Gharrett et al., 2012; Kamin et al., 2014). These 2 characteristics of their life history appear to be somewhat in conflict, in that species with the potential for long-distance dispersal would not be expected to have restricted geographic dissemination. However, results of a study of 11 microsatellite loci of northern rockfish captured along the range of this species in the Bering Sea and Aleutian Islands of Alaska reveal a significant isolation-by-distance relationship, indicating limited lifetime dispersal of between approximately 12 and 120 km for this species (Gharrett et al., 2012). Reduced currents downstream of coral habitat (and potentially other highly structured habitats) may provide a process for larval rockfish to be retained near where they were spawned, creating an important mechanistic link between the known genetic structure of northern rockfish and restricted dispersal.

This unique observation of a larval northern rockfish in deep-sea coral habitat improves our knowledge of the early life history of this commercially important species and may provide insight into a potential mechanism for larval retention for a taxonomic group that has a high degree of population structure and limited lifetime dispersal. The result also highlights the further importance of deepwater coral habitat as essential habitat for rockfishes.

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Interactions, injuries, and mortalities of killer whales (*Orcinus orca*) observed during fishing operations in Alaska

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Abstract—Fishery observer records from 2001 through 2016 were examined to document interactions, injuries, and mortalities of killer whales (*Orcinus orca*) associated with fishing operations in Alaska. Although widespread throughout Alaska, the highest numbers of such events occurred in the southeastern Bering Sea. Killer whales of the resident ecotype feeding on catch or discarded catch and fishermen using whale deterrence measures represented 96% (number of interactions [*n*]=3110) of all interactions examined in this study (*n*=3245). We found that 87% (*n*=2817) of all interactions occurred during longline operations. Both minor and serious injuries were documented. Twenty-seven killer whales were reported dead, but additional mortalities are assumed. Most whales killed were residents; however, 3 transient whales were also taken. Because killer whale populations are relatively small, a low level of mortality may significantly affect populations, especially if multiple sympatric stocks are shown to exist. Given the long history (i.e., over 6 decades) that Alaska killer whales have had with fishing operations, it is likely that these interactions will continue.

Throughout the world's oceans, interactions of killer whales (*Orcinus orca*) with fishing operations have been well documented (Visser, 2000; Purves et al., 2004; Dalla Rosa and Secchi, 2007; Roche et al., 2007; Clark and Agnew, 2010; Tixier et al., 2010; Belonovich and Burkanov, 2012; Tixier et al., 2016). In Alaska, Japanese fishermen first reported depredation by killer whales on longline catches of groundfish in the early 1960s (Dahlheim[1]). Throughout the 1980s, fishermen operating in the United States reported depredation by killer whales on their longline catches (Dahlheim[1]), with additional reports provided by both industry and fishery observers. Interactions have included depredation of longline-caught fish by killer whales, the presence of killer whales feeding off discards in other fisheries, and instances of fishermen using deterrence (Dahlheim[1]).

Killer whales are widely distributed and commonly encountered throughout the waters of Alaska (Braham and Dahlheim, 1982; Zerbini et al., 2007). Three ecotypes of killer whales have been reported from Alaska: resident, transient, and offshore ecotypes. Ecotypes differ in external morphology, acoustic behavior, and prey preferences (Baird and Stacey, 1988; Baird and Dill, 1995; Ford et al., 1998; Dahlheim et al., 2008). External morphology (i.e., fin or saddle shape) combined with natural and human-induced scaring allows for individual, and therefore group, and ecotype identification (Bigg et al., 1990; Emmons et al., 2019). Animals with such identifiable marks can be tracked through time, allowing researchers to document injuries to individual whales, assess individual and group movements, and identify the ecotype involved in specific fishery interactions.

Interactions between killer whales and fisheries affect both fishermen and the individuals or pods of killer whales

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[1] Dahlheim, M. E. 1988. Killer whale (*Orcinus orca*) depredation on longline catches of sablefish (*Anoplopoma fimbria*) in Alaskan waters. NWAFC Processed Rep. 88-14, 31 p. [Available from Alsk. Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.]

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that are involved in the interactions. Financial losses are incurred by fishermen as a result of lost or damaged gear, lost fishing time due to having to wait for depredating killer whales to leave the vicinity of fishing gear, catch degradation due to increased gear soak time, and overall reduction in harvest of fish (Yano and Dahlheim, 1995; Tixier et al., 2020). In addition to negative effects to the fishing industry, direct interactions between killer whales and fishing vessels have resulted in whales being seriously injured or killed.

Here we summarize data collected by the National Marine Fisheries Service (NMFS) North Pacific Observer Program on fishery interactions of killer whales in the waters of the Bering Sea, Aleutian Islands, and Gulf of Alaska (GOA) during 2001–2016.

Materials and methods

Background

The Marine Mammal Protection Act of 1972, Public Law 92-522, title 1, section 118, requires the NMFS to classify all U.S. commercial fisheries into 1 of 3 categories based on the level of incidental mortality and serious injury of marine mammals occurring in those fisheries (Marine . . . 2020). There are 23 groundfish fisheries operating in the Bering Sea, Aleutian Islands, and GOA that are defined in the List of Fisheries (LOF; see Breiwick, 2013) for which marine mammal bycatch must be estimated (for additional information, see table 1 in the NMFS Office of Protected Resources List of Fisheries Summary Tables, available from website). These fisheries target different fish species by using trawl gear (9 fisheries), longline gear (10 fisheries), and pot gear (4 fisheries). We used this LOF and data from the NMFS North Pacific Observer Program to assess fisheries interactions with killer whales from 2001 (the earliest year in which observer data can be assigned to a particular fishery) through 2016.

Observer program data collection

The North Pacific Observer Program is the largest fisheries observer program in the United States (NMFS, 2013). The NMFS Alaska Fisheries Science Center's Fisheries Monitoring and Analysis Division is responsible for administering this program, which includes observer training, logistics, data management, and analyses. Up to 220 observers are deployed at any one time to collect data for use by the NMFS in managing the Alaska groundfish fisheries. The collected data are critical to NMFS fish stock assessments and to efforts to monitor commercial fishing activities throughout the U.S. exclusive economic zone in the North Pacific Ocean (Fig. 1) as required by the Magnuson-Stevens Fishery Conservation and Management Act (Magnuson-Stevens . . . 2020). At the request of the Alaska Fisheries Science Center's Marine Mammal Laboratory (MML), observers record information on sightings of marine mammals and document fishery interactions, injuries, and mortalities of killer whales.

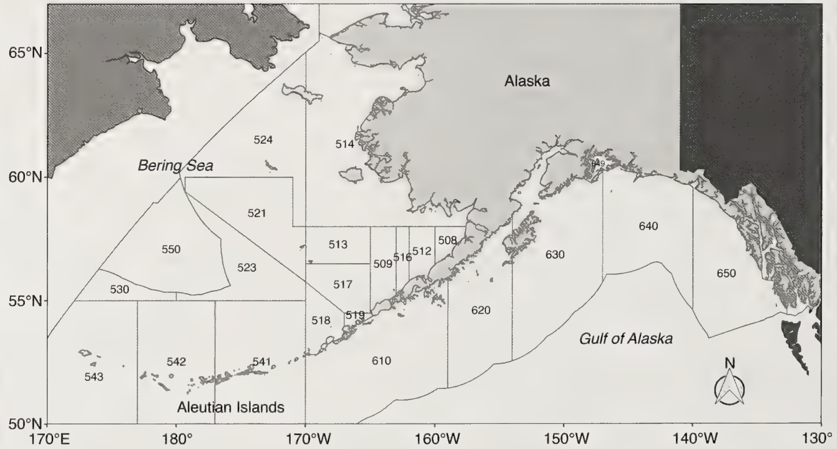

Figure 1

Map of the National Marine Fisheries Service reporting areas in the U.S. exclusive economic zone in the North Pacific Ocean, identified by numbers and outlined with gray lines, where commercial fishing activities are monitored.

The North Pacific Observer Program uses a stratified, hierarchical sampling design to monitor fishing activities in the U.S. exclusive economic zone in Alaska. From the development of domestic fisheries in the early 1990s until the restructuring of the North Pacific Observer Program in 2013, large vessels over 38.1 m (125 ft) in length overall were required to carry an observer on all fishing trips (this group of vessels is the *full-coverage* pool) and vessels between 18.2 m (60 ft) and 37.9 m (124.5 ft) length overall were required to carry observers on approximately 30% of their fishing days (this group of vessels is the *partial-coverage* pool). The restructuring of the North Pacific Observer Program in 2013 redefined these pools such that the full-coverage pool consists primarily of vessels that process catch at sea (catcher-processors and motherships) and vessels that participate in catch share programs regardless of vessel size and such that the partial-coverage pool consists primarily of vessels that deliver their catch to shoreside processors and are over 12.2 m (40 ft) length overall (NPFMC[2]). Observer deployment rates for partial-coverage vessels have varied with management needs for various fisheries and are set each year in an annual deployment plan (e.g., NMFS[3]). These changes over time are one of the reasons that analyses and results are presented separately for the full-coverage and partial-coverage pools.

Once an observer is on a vessel, a subset of hauls are randomly selected to be sampled for catch composition and other biological catch data (Cahalan et al., 2014; Cahalan and Faunce, 2020). If a marine mammal is caught, the observer records this event regardless of whether the animal is within the selected hauls; for marine mammal bycatch, observers record all known mortalities. Sightings of and fishery interactions with marine mammals are also recorded; whenever the observer becomes aware of the presence of a marine mammal, data for the interaction or sighting are recorded.

Interactions of marine mammals with fishing vessels and fishing gear are recorded by observers according to the 7 broad categories defined in the observer manual (e.g., AFSC[4,5]). These categories are as follows: 1) some form of deterrence was used to discourage nearby mammals from interacting with fishing operations, 2) a mammal was entangled and released without trailing gear, 3) a mammal was entangled and released with trailing gear, 4) a mammal was lethally removed (from gear that was not trailing), 5) a mammal boarded the vessel, 6) a mammal was feeding on catch that had not yet been landed, and 7) a mammal was feeding on discards.

During the course of this study (2001–2016), observers used all of these interaction categories with the exception of the category for mammals feeding on discards because it was not introduced until 2008. Observers also used additional interaction categories recorded as *other* (i.e., observations that did not fit the 7 categories listed above) and *unknown* (i.e., interactions observed by the vessel crew but not seen by the observer). In addition, mortalities were recorded and classified as follows: 1) killed by gear, 2) killed by propeller, 3) removed lethally from trailing gear (crew killed a mammal entangled in gear), or 4) removed lethally from gear that was not trailing (in spite of efforts by the crew to release the mammal, the animal died). For whales entangled in gear and subsequently released, an assessment was made by scientists at the MML to determine if the injury sustained would result in the whale's death. If there was a high probability that the entanglement would result in the death of the whale, the incident was listed as a serious injury (serious injury criterion are further described in NMFS[6]).

Analysis of fisheries interactions

The data on fisheries interactions and marine mammal sightings collected by observers were summarized within sampling strata and fisheries as defined in the LOF. The fishery in which a haul or set occurs is determined by the NMFS reporting area (Fig. 1), gear type, and trip target code (dominant species retained; for additional detail, see Cahalan et al., 2014). Additional information collected for an interaction with one or more marine mammals may include the date, year, latitude, longitude, number of animals, vessel and observer identifiers, indication of whether photographs were taken, and indication of whether tissue samples were taken (Breiwick, 2013).

Between 2001 and 2016, the number of hauls monitored by observers fluctuated with varying coverage rates and fishing effort; however, these changes were not always consistent with changes in fishing effort. Therefore, numbers of sampled hauls for which associated interactions with killer whales have been recorded have to be considered in the context of these changes in sampling intensity (for summary of annual sampling intensity, see table 1-1 in AFSC and ARO[7]). As a result, some fisheries, gears, vessel types, and years are represented in the database at higher rates because of differential rates of observer deployment (full coverage versus partial coverage or interannual changes in coverage; see AFSC and ARO[7]). Combining data from different sampling strata without correcting for coverage rates will result in biases toward those areas of the fishery with higher observer coverage.

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[2] NPFMC (North Pacific Fishery Management Council). 2011. Environmental assessment/regulatory impact review/initial regulatory flexibility analysis for proposed amendment 86 to the fishery management plan for groundfish of the Bering Sea/Aleutian Islands management area and amendment 76 to the fishery management plan for groundfish of the Gulf of Alaska. Restructuring the program for observer procurement and deployment in the North Pacific, 239 p. North Pac. Fish. Mange. Counc., Anchorage, AK. [Secretarial review draft.] [Available from website.]

[3] NMFS (National Marine Fisheries Service). 2017. 2018 annual deployment plan for observers and electronic monitoring in the groundfish and halibut fisheries off Alaska, 20 p. Natl. Mar. Fish. Serv., Juneau, AK. [Available from website.]

[4] AFSC (Alaska Fisheries Science Center). 2001. North Pacific groundfish observer manual, 571 p. [Available from North Pac. Groundf. Obs. Program, Alsk. Fish. Sci. Cent., Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115.]

[5] AFSC (Alaska Fisheries Science Center). 2021. 2022 observer sampling manual, 496 p. Fish. Monit. Anal. Div. and North Pac. Groundf. Obs. Program, Alsk. Fish. Sci. Cent., Natl. Mar. Fish. Serv., Seattle, WA. [Available from website.]

[6] NMFS (National Marine Fisheries Service). 2014. Process for distinguishing serious from non-serious injury of marine mammals. Natl. Mar. Fish. Serv. Policy Directive 02-238, 4 p. [Available from website.]

[7] AFSC (Alaska Fisheries Science Center) and ARO (Alaska Regional Office). 2018. North Pacific Observer Program 2017 annual report. AFSC Processed Rep. 2018-02, 136 p. [Available from website.]

Because of these differential coverage rates and the limited information on fishing effort from the unobserved portion of the fisheries, it is not possible to use the number of sampled hauls (nor the number of sampled trips) and the total number of hauls (nor the total number of trips) to obtain a direct estimate of the total number of interactions that occur for all fisheries. A proxy for the ratio of sampled hauls to total hauls has been used to estimate mortality of marine mammals by assuming that the weight of groundfish from sampled hauls (as determined by the observer during sampling), as a fraction of the total groundfish weight landed and reported on fish tickets for the stratum (year, fishery, area, and marine mammal species), is equal to the ratio of the number of sampled hauls to the total number of hauls in the stratum. This approach is typical for estimating incidental mortality in an observed fishery (Breiwick, 2013); however, we have not used this approach in this analysis for several reasons detailed later in the text.

Our focus was to examine only interactions that occurred on observed hauls, not to estimate the total number of the various interaction types in each fishery. Interactions recorded by observers may occur on hauls that are not scheduled for sampling but during which the crew notifies the observer of an interaction. The number of hauls monitored for interactions includes these hauls in addition to hauls randomly selected to be sampled (and monitored for interactions with mammals), and as a result the number of monitored hauls may be greater than the number of sampled hauls, increasing the nominal monitoring rate relative to the rate associated with the randomized sampling design. Although the number of animals involved is recorded by the observer, some animals present might not be observable (e.g., swimming below the surface or otherwise out of sight of the observer). In addition, multiple animals may be involved in any interaction, and some animals may be included in counts associated with different interaction types. Lastly, interactions are not necessarily independent of each other on a haul or within a trip. For example, in cases where deterrence is used to decrease depredation by mammals on the catch, feeding on catch or feeding on discards may also be recorded (i.e., for a single haul, 3 interactions, each of a different type and each involving multiple animals, may be recorded).

For the reasons given in a previous paragraph, we have not used ratio estimates based on groundfish weights to make inferences about interactions of marine mammals with fishing gear for all fishing events in Alaska. We have, however, summarized the frequency of interactions, taking into account the changes that occurred in observer coverage throughout the years by comparing the percentage of monitored hauls in which interactions were documented for the full-coverage and partial-coverage strata separately, although sampling rates in partial-coverage strata have varied between years after 2013 and varied by gear types in 2016 (AFSC and ARO[7]).

The percentage of hauls in which interactions with killer whales occurred was computed as the number of hauls in which at least one interaction (of any type) was recorded divided by the number of hauls monitored by observers (multiplied by 100), an estimate of hauls with killer whale interactions per 100 monitored hauls. This estimate is inclusive of hauls that were not sampled but during which the observer or the vessel crew noted an interaction. These percentages were computed for each year and for the partial- and full-coverage strata separately. By presenting the percentage of hauls with interactions for each sampling stratum, the analysis also accounts for differences in sampling intensity. Interactions with killer whales that were recorded for trips that were not associated with a specific haul were not included in this analysis (39 interactions of the 3245 interactions recorded since 2008).

About the tables and figures of this article in which numbers of interactions are used, it should be noted that the number of interactions with killer whales is more than the number of hauls with such interactions. As noted here previously, this difference results from some hauls (fewer than 10%) having multiple interactions recorded (e.g., a killer whale or group of killer whales may be classified as feeding on discards as well as having the vessel crew use a deterrence toward it). The number of interactions in these tables is not adjusted for sampling rate. The mean between-year percentages of hauls with interactions were computed as the simple average between years for a specified set of covariates. For example, the mean percentage of hauls with interactions for each month was computed as the mean between years of the percentage of interactions for each month. Because we are interested in comparisons between months of the expected monthly percentage of hauls where interactions occur, we use the between-year mean, weighting monthly estimates for each year equally. Alternatively, use of a weighted mean would support inferences about the probability of an interaction with a mammal being recorded for a haul in a given month, but that is not our aim here.

Photographic collection and analyses

Beginning in 1986, observers were instructed to take photographs of killer whales that were sighted either close to fishing vessels or actively interacting with fishing operations. We analyzed all photographic materials (in all forms: film, digital, and video) collected from 1986 through 2015 to determine the killer whale ecotype involved in the fishery interactions that occurred in Alaska. A narrative was completed for each interaction, and the narratives include the observer's cruise number, haul number, observer's name, date, location, interaction code, number of whales present, and details summarizing whale behavior.

Only those images that were in focus, had adequate lighting, and were of a quality high enough to accurately identify an individual killer whale or the ecotype involved (i.e., shape of dorsal fin or saddle patch, whale markings, and clearly visible scars) were used in the analyses. Determination of killer whale ecotype was done by examining a whale's external morphology (i.e., fin shape and size and shape of saddle patch), by comparing the photographic data to images of known Alaska killer whale ecotypes (i.e., images in Dahlheim, 1997, and in unpublished catalogs maintained by both the MML and the North Gulf Oceanic Society. In addition, different ecotypes of killer whales do not intermix. If unknown whales are seen with known members of a resident pod, those unknown whales (linked by association) are considered residents. Photographic data were also used to document injuries and mortalities of killer whales. Any dead killer whale (either killed directly in a fishing operation or found floating at sea) was brought on board the fishing vessel to be photographed and examined by the observer. Whenever possible, the dead animal's sex, age class (i.e., calf, juvenile, or adult) was determined and external measurements were collected (AFSC[4,5]). The results of a review of the observer's photographs and associated interaction form provide information on the plausible cause of death.

Tissue collection and genetic analyses

In 1999, the Cetacean Tissue Collection project was initiated by the MML through requests made to observers to collect tissue samples from any dead cetacean brought aboard a fishing vessel by using MML-provided sampling kits; written instructions were included in the observer manual (see AFSC[4]). When possible, an 8-cm^3 sample of skin and blubber was obtained from each carcass. The samples were stored in a vial containing buffered salt solution with dimethyl sulfoxide and labeled with the observer's cruise number and the date, location, and detailed circumstances related to the event (e.g., cause of death when possible, location on the whale's body where sample was taken, whale measurements, and carcass condition). With the exception of 2 tissue collections (biopsies) taken from live whales, all tissues collected were taken from dead whales that were brought on board the vessel.

Genetic samples from killer whales were analyzed at the NMFS Southwest Fisheries Science Center. Genetic results include species verification, sex determination, and when possible, identification of the killer whale ecotype. Results of the analyses were returned to the MML to update the Cetacean Tissue Collection database and to assign the injured or dead animal to a particular stock. Genetic results were also forwarded to staff members of the NMFS Alaska Regional Office to provide them with vital information for assessing the effects to a specific killer whale ecotype or stock.

Results

Fishery interactions

Between 2001 and 2016, observers reported 3245 (2415 in full-coverage strata) fishery interactions with killer whales from 16 NMFS reporting areas ranging from the Bering Sea, throughout the Aleutian Islands, and eastward into Southeast Alaska (Fig.1). There were 3026 hauls (2268 in full-coverage strata) during which at least one interaction occurred (Suppl. Table 1A) (online only) out of the 680,872 hauls (534,601 in full-coverage strata) that occurred on observed trips over the 16-year period. The percentage of the hauls for which interactions with killer whales were reported varied by area, with the highest percentage of hauls with interactions occurring in the Bering Sea (Fig. 2, Suppl. Table 1B [online only]). Interactions with killer whales also varied by year within each area (Suppl. Table 1, A and B) (online only), by month or season (Fig. 3), and by type of interaction (Fig. 4).

Killer whales feeding on catch before the catch was landed, killer whales feeding on discards, and vessel crew members using varied methods of whale deterrence represented 96% of all observed interactions recorded, and these interaction types consistently accounted for higher percentages of affected hauls than other interaction types (Suppl. Table 2, A and B) (online only). Feeding on catch that had not yet been landed was the most common interaction documented during this study. Feeding on discards was known to occur prior to 2008, on the basis of records maintained by MML staff; however, this whale behavior was not formally documented by observers until 2008. Figure 4 shows that the use of deterrence methods was relatively low for the years prior to 2008 and that the frequency of deterrent use appears to have increased in more recent years. The areas in which these 3 types of interactions occurred by season is depicted in Figure 5.

We found that 2527 hauls (84%) with at least one interaction with killer whales occurred during longline operations (Suppl. Table 3A) (online only). Longline operations in the Bering Sea and Aleutian Islands (BSAI) accounted for 2130 hauls (84%) with interactions, whereas longline fisheries in the GOA represented only 397 hauls (13%) with interactions (Suppl. Table 3A) (online only). There were 56 hauls with interactions with killer whales that were assigned to the *unknown* fishery category (for 38 hauls of longlines and for 18 hauls of trawl gear, the collected data corresponds to none of the fisheries in the LOF). An additional 38 hauls could not be categorized to a specific fishery because the necessary data were not available.

Interactions with killer whales were also reported for trawl operations in the BSAI and GOA, during which 322 hauls with interactions (11%) were documented over the 16-year period (Suppl. Table 3A) (online only). The greatest number of interactions occurred in the BSAI flatfish trawl fishery (n=272). Few, if any, interactions occurred in the fishery that uses non-pelagic trawl gear.

The operations of the pot gear fishery that targets sablefish in the BSAI logged 82 hauls with at least one interaction over the entire period (Suppl. Table 3A) (online only). The

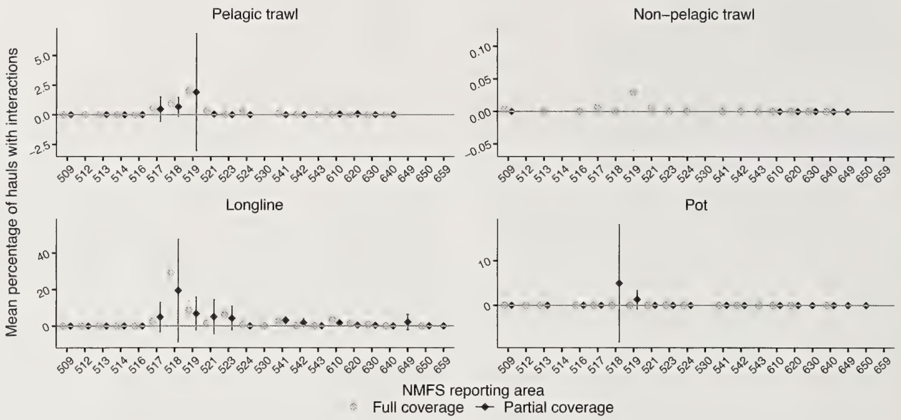


Figure 2

Mean percentage of monitored hauls with recorded interactions of killer whales (*Orcinus orca*) with fishery operations across the years of 2001–2016, by gear type, category of observer coverage (full and partial), and National Marine Fisheries Service (NMFS) reporting area in the U.S. exclusive economic zone in the North Pacific Ocean. Error bars indicate ±1 standard deviation. Note that the scale of the *y*-axis (percentage of monitored hauls) varies among panels.

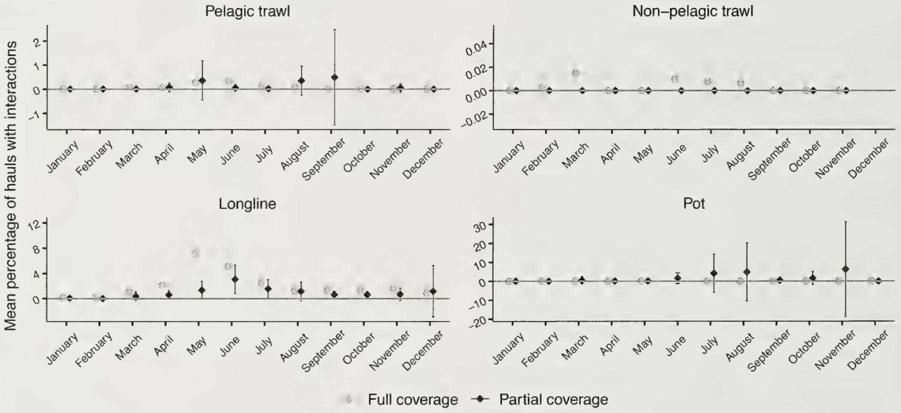


Figure 3

Mean percentage of monitored hauls with recorded interactions of killer whales (*Orcinus orca*) with fishery operations across the years of 2001–2016, by gear type, category of observer coverage (full and partial), and month, in the waters of the Bering Sea, Aleutian Islands, and Gulf of Alaska. Error bars indicate ±1 standard deviation. Note that the scale of the *y*-axis (percentage of monitored hauls) varies among panels.

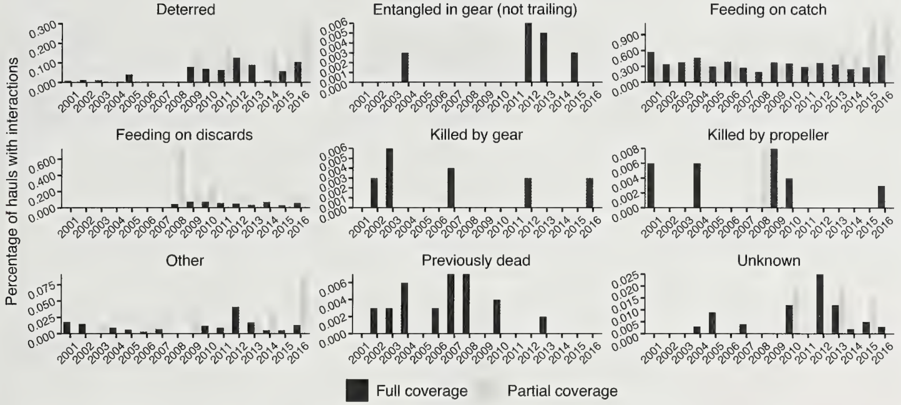


Figure 4

Percentage of monitored hauls with recorded interactions of killer whales (*Orcinus orca*) with fishery operations from 2001 through 2016, by type of interaction, category of observer coverage (full or partial), and year, in the waters of the Bering Sea, Aleutian Islands, and Gulf of Alaska. Note that the scale of the *y*-axis (percentage of monitored hauls) varies among panels.

number of hauls with interactions with killer whales in the pot gear fishery notably increased after 2008 because of the inclusion of a new interaction code (i.e., feeding off discards) that was reported from a few pot vessels.

The number of monitored hauls varied by year and sampling stratum. Given the low numbers of hauls that were monitored during their operations, the BSAI rockfish longline fishery (137 hauls for all years), GOA flatfish longline fishery (43 hauls for all years), and GOA rockfish longline fishery (28 hauls for all years) were not included in the fishery-specific graphs presented here. The following fisheries for which no interactions were reported were also excluded from the analysis: the BSAI Pacific cod pot, GOA pollock trawl, Alaska GOA rockfish trawl, and GOA Pacific cod pot fisheries. Data for all fisheries are summarized in Supplementary Table 3, A and B (online only), and in Figures 6 and 7.

Injuries

Photographic images were reviewed to document the types of injuries seen on Alaska killer whales. Relatively few injuries were directly witnessed by observers, and most of the photographs depicted old injuries. Similar to the injuries observed in other populations of killer whales, the minor injuries we documented include the following: body scratches or nicks on the trailing edge of the dorsal fin that resulted from interactions with either conspecifics or prey items; wounds caused by attachments of cookiecutter sharks (*Isistius brasiliensis*), Pacific hagfish (*Eptatretus stoutii*), or barnacles; and small wounds made during prior biopsy sampling or satellite tagging research. Killer whales with more severe injuries were also photo-documented by observers. The top of the dorsal fin of several killer whales appeared to be injured or missing. At least 3 large males were seen with dorsal fins that were completely flopped over; one of these whales also had severe spinal damage. Most injuries appeared to be healed, indicating that a previous injury had occurred. However, the most severe injury was that of a killer whale whose dorsal fin had been completely cut off and who had severe damage to its head and lateral region; photographs of this animal were collected as it fed on discards (Fig. 8, A and B).

Mortalities

Between 1991 and 2016, 24 dead killer whales were reported by NMFS observers, and all of these dead animals were observed in the Bering Sea, 23 of them in the full-coverage stratum. Of the 24 dead whales, 14 animals were killed by fishing gear and 10 whales were killed by propellers (Table 1). Of the 14 mortalities associated with fishing gear, 7 deaths resulted from entanglements in longline gear (Fig. 9) and 7 deaths occurred during trawling operations. For the 10 killer whales killed by propellers, all mortalities resulted from interactions with flatfish, rockfish, or Atka mackerel trawl operations. Deaths of killer whales were reported for 6 of the 23 observed fisheries: the BSAI flatfish trawl, BSAI pollock trawl, BSAI rockfish trawl, BSAI Atka mackerel trawl, BSAI Greenland turbot longline, and BSAI Pacific cod longline fisheries.

Five reports documented live killer whales entangled in gear (Table 2). In all cases, the killer whales were

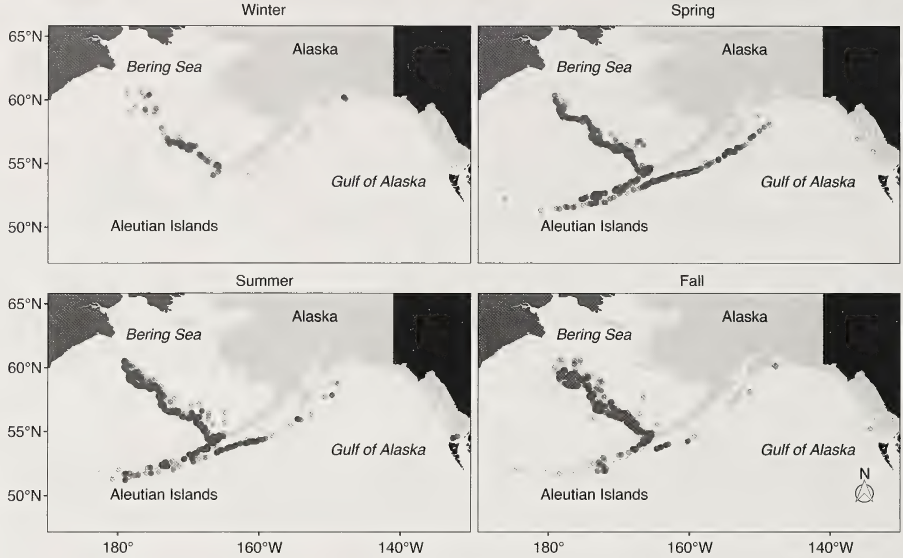


Figure 5

Map of locations, by season, where observers on board fishing vessels recorded that killer whales (*Orcinus orca*) were feeding off catch or discards or that deterrence was used during 2001–2016 in the waters of the Bering Sea, Aleutian Islands, and Gulf of Alaska. The seasons are as follows: December, January, and February (winter); March, April, and May (spring); June, July, and August (summer); and September, October, and November (fall).

subsequently released with the hopes that they would survive. A determination of serious injury (i.e., an entanglement that ultimately results in the death of the whale) was made for 3 whales caught in trawl gear, raising the total number of dead killer whales to 27 for the period between 1991 and 2016.

In addition to the deaths documented as a result of killer whales interacting with the fishery, observers reported 16 dead killer whales (Table 1) that had died prior to the recorded fishery interaction. Three of these whales were observed during longline operations, and 13 were reported during trawl operations. The level of decomposition of the previously dead whales varied from minor (suggesting the whale recently died) to considerable decomposition.

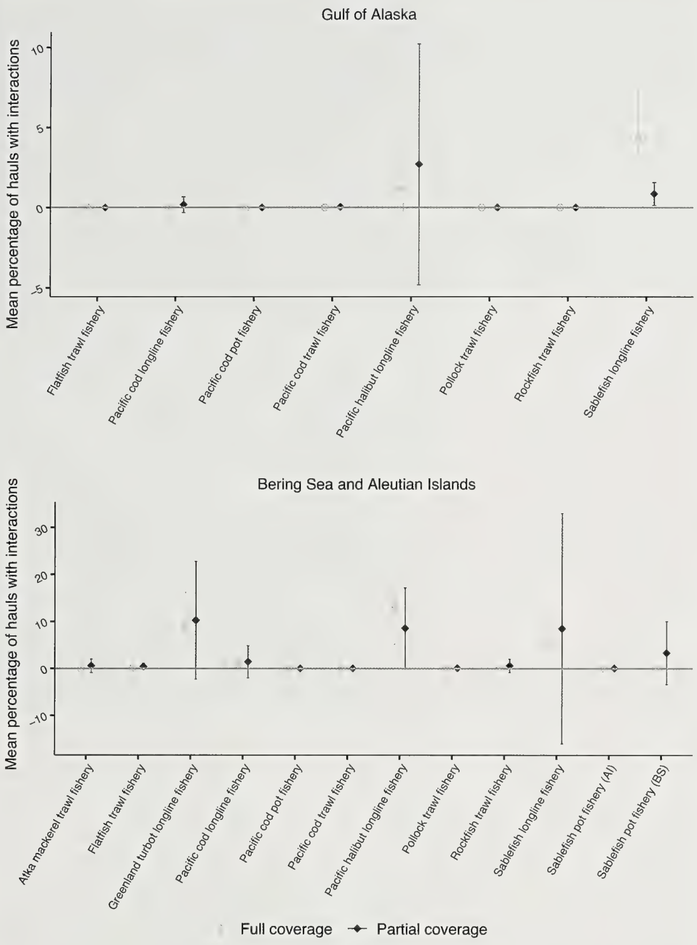
Ecotype

From 1986 through 2015, a total of 9828 photographs of killer whales (2643 images of sufficient quality for analysis) were collected during 375 observed cruises and were reviewed to determine the killer whale ecotype. During longline fishing operations, photographs of killer whales were collected during 266 cruises in the same period (1986–2015), and 1955 images of sufficient quality were reviewed. For the examined photographs from longline cruises, all depredation events were associated with the resident killer whale ecotype. Individuals from all age classes (from calves to adults) and from both sexes of killer whales can be seen close to the vessels in photographs taken during these depredation events.

For the 109 cruises that occurred in 2008–2014, after the interaction type for feeding on discards was added, 688 images of killer whales of sufficient quality were reviewed. The resident killer whale ecotype accounted for all the discard interactions associated with fishing operations. Again, individuals from all age classes and both sexes of killer whales can be seen close to the vessel in photographs taken during these events of discard feeding. No photographs of killer whales of the live transient ecotype were collected during this study.

Genetic analysis

Seven samples from killer whales representing animals killed by gear or by propeller were collected and available for genetic analysis (Table 3). Genetic analysis identified



Gulf of Alaska

Bering Sea and Aleutian Islands

Figure 6

Mean percentage of monitored hauls with recorded interactions of killer whales (*Orcinus orca*) with fishery operations across the years of 2001–2016, by fishery and category of observer coverage (full or partial), in the Gulf of Alaska and in the Bering Sea (BS) and Aleutian Islands (AI). Fisheries are among those groundfish fisheries defined in the List of Fisheries of the Office of Protected Resources, National Marine Fisheries Service. Error bars indicate ±1 standard deviation.

4 of the whales as being from the Alaska resident stock and 3 of the whales as being from the Alaska transient GOA-BSAI stock. Three resident killer whales died as a result of interactions with the BSAI flatfish trawl fishery (killed by propeller), and the other resident whale died during BSAI Pacific cod longline operations (killed by gear). The 3 dead transient whales were killed as a result of interactions with the BSAI pollock trawl fishery (all killed by gear). Six of the animals killed were listed as juveniles of both sexes; the seventh killer whale was an

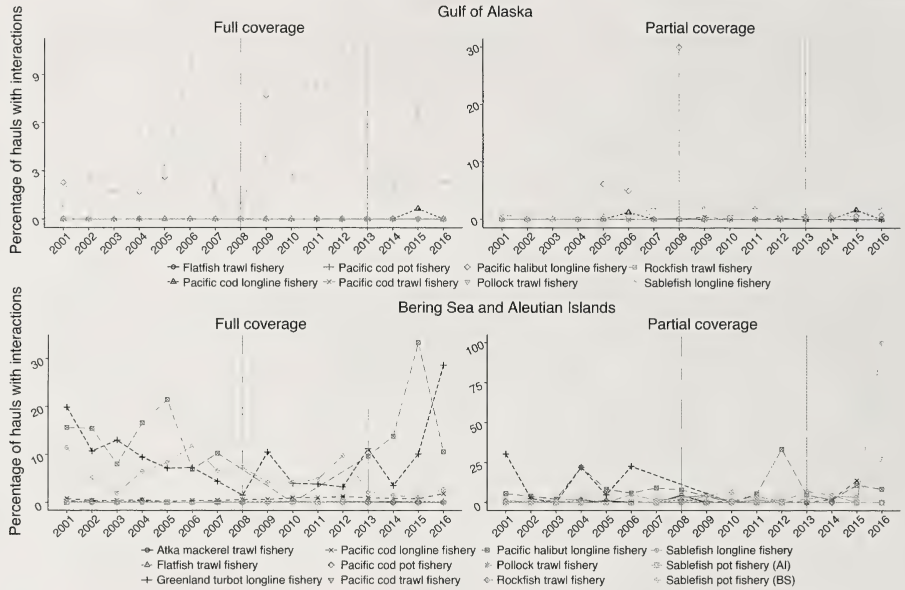


Figure 7

Percentage of monitored hauls with recorded interactions of killer whales (*Orcinus orca*) with fishery operations from 2001 through 2016, by fishery, category of observer coverage (full or partial), and year, in the Gulf of Alaska and in the Bering Sea and Aleutian Islands. Fisheries are among those Alaska fisheries defined in the List of Fisheries of the Office of Protected Resources, National Marine Fisheries Service. Vertical lines are shown as references for the addition in 2008 of "feeding on discarded catch" to the list of interaction types recorded by observers and for the restructuring in 2013 of the North Pacific Observer Program.

adult female (size was not specified). Two tissue samples were also collected from decomposed killer whales that were brought on board the vessel. Results of genetic analysis indicate that both samples were from juvenile males of the resident ecotype.

Additional samples were available for analysis during this study. Staff members of the MML authorized an observer to biopsy killer whales by using darts as they fed on catch during BSAI sablefish longline operations. Two samples were collected; results of genetic analysis confirm that the samples are from killer whales of the resident ecotype.

Discussion

Although fishery interactions with killer whales were widespread throughout Alaska, most interactions were reported during fishing operations in the southeastern Bering Sea, from the Aleutian Islands north along the shelf break to areas north and west of St. Matthews Island. When comparing this area with locations where interactions occurred during the 1980s and 1990s (Dahlheim[1]; Yano and Dahlheim, 1995), we found that the southeastern Bering Sea continues to be a hotspot for interactions of killer whales with fisheries. Recent data indicate that interactions have occurred as far north as St. Matthews Island and as far west as Agattu Island (just southeast of Attu Island, which like Agattu Island is part of the Near Islands, a group of islands in the Aleutian Islands), with reports from both the Bering Sea and Pacific Ocean sides of the Aleutian Islands. Interactions also occurred along the south side of the Alaska Peninsula into the western GOA near Kodiak, Alaska, with 2 reports as far east as Southeast Alaska. Results of the decadal comparisons of the locations of these interactions indicate that a range expansion could be occurring.

In previous longline depredation studies, killer whales have been reported to consume sablefish (*Anoplopoma fimbria*), Greenland halibut (*Reinhardtius hippoglossoides*), arrowtooth flounder (*Atheresthes stomias*), Pacific halibut (*Hippoglossus stenolepis*), and searcher (*Bathymaster*

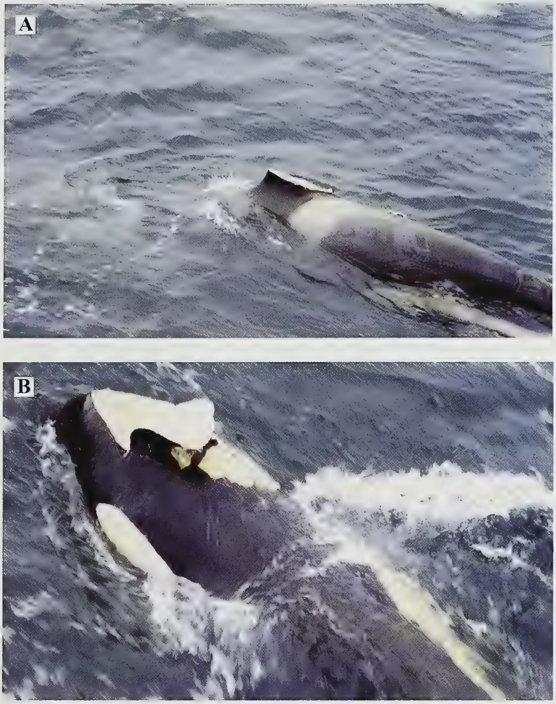


Figure 8

Photographs of a killer whale (*Orcinus orca*) (**A**) with a cut-off dorsal fin and (**B**) with severe head and lateral injuries in the Bering Sea. The photographs were taken as the whale fed off discards during the fishing season in 1994.

signatus) (Dahlheim[1]; Yano and Dahlheim, 1995). Because these data have not been extrapolated to cover interactions for the entire fleet, the number of interactions reported here is an underestimate of the total number of interactions with killer whales occurring in the Alaska groundfish fishery.

During groundfish trawl operations, resident killer whales were seen in close proximity (<3 m) to fishing vessels and feeding off a variety of fish being discarded from the vessels. Group size varied for killer whales, and all age classes were seen taking part in this feeding. We have received multiple reports from fishery observers of both individual and groups of killer whales following vessels for extended periods (i.e., periods ranging from 3 d to 28 d).

Over the past 6 decades (from the 1960s to the 2020s) in Alaska, fishermen have attempted to either reduce or eliminate depredation by killer whales through the use of different deterrence methods (see Dahlheim[1]). Although most deterrence efforts occurred during longline depredation events, reports of killer whales being shot while feeding off discards has also been documented during longline operations. Despite this long-term work by fishermen to protect their catch and reduce their financial losses, interactions continue to occur.

We identified the resident killer whale ecotype as the ecotype responsible for all the interactions reported during this study, on the basis of the external morphologic characteristics of whales of this ecotype, genetic data, photographic matches made to well-known resident killer whales, and the recognition of one distinctly marked individual as a resident killer whale that linked all killer whales by association to that ecotype. Little information is known about the seasonal occurrence and movements of resident killer whales. We documented that interactions were occurring every year and month, with the highest number of interactions reported during the spring and summer months. Given that fishery interactions with resident killer whales are reported throughout the year, we now know that killer whales occur in these northern areas year-round. Photographic matches of individual killer whales collected by observers between 1987 and 2001 (Dahlheim et al., 2002) at locations in the Pacific Ocean and the Bering Sea indicate that resident killer whales moved from south of Unimak Pass, north into the Bering Sea along the shelf break, and then to waters west of St. Matthews Island. Movements by individual killer whales also occurred from Unimak Pass westward to the central Aleutian Islands and then north into the Bering Sea to waters west of St. Matthews Island.

Killer whales occur in high densities throughout Alaska (Leatherwood and Dahlheim[8]). Zerbini et al. (2007), on the basis of surveys of the nearshore waters of the GAO and the Aleutian Islands, estimated abundance of resident killer whales at 991 individuals (coefficient of variation=0.52), with a 95% confidence interval of 380–2585 individuals. Based on photo-identification research conducted by the MML and the North Gulf Oceanic Society in the Bering Sea and western GOA during 2001–2012, a minimum count of western Alaska residents is 1475 killer whales (Muto et al., 2016). Of this total count, the percentage of killer whales or pods involved with fishery interactions

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[8] Leatherwood, S. J., and M. E. Dahlheim. 1978. Worldwide distribution of pilot whales and killer whales. Nav. Ocean Syst. Cent., Tech. Rep. 295, 39 p. [Available from website.]

Table 1

Observed mortalities of killer whales (*Orcinus orca*) recorded from 1991 through 2016 by observers aboard vessels in various Alaska Bering Sea and Aleutian Islands fisheries.

	No. of individuals (fishery)		
Year	Killed by gear	Killed by propeller	Previously dead
1991	1 (pollock trawl)		
1992	1 (pollock trawl)		
1993	1 (flatfish trawl)		
1994			
1995	1 (Pacific cod longline)		1 (flatfish trawl)
1996			1 (flatfish trawl)
1997	1 (pollock trawl)		
1998		1 (flatfish trawl)	1 (flatfish trawl)
1999	1 (Greenland turbot longline; 1 (pollock trawl)		1 (pollock trawl)
2000			1 (Pacific cod longline)
2001		2 (flatfish trawl)	
2002	1 (pollock trawl)		1 (flatfish trawl)
2003	1 (pollock trawl); 1 (Pacific cod longline)		1 (pollock trawl)
2004		2 (flatfish trawl)	1 (flatfish trawl); 1 (Pacific cod trawl)
2005			
2006			1 (flatfish trawl)
2007	1 (Greenland turbot longline)		1 (Atka mackerel trawl); 1 (Pacific cod trawl)
2008		1 (flafish trawl)	2 (Pacific cod trawl)
2009		2 (Atka mackerel trawl)	
2010		1 (rockfish trawl)	1 (Pacific cod longline)
2011			
2012	1 (Pacific cod longline)		
2013			1 (Pacfic cod longline)
2014			
2015	1 (Greenland turbot longline)		
2016	1 (Pacific cod longline)	1 (flatfish trawl)	
Fishery type		No. of individuals	
Trawl	7	10	13
Longline	7	0	3
Total	14	10	16

is unknown. Resident killer whales are very social animals that occur in distinct, stable pods. During periods of socialization and foraging, resident pods are known to join other resident pods temporarily (Bigg et al., 1990). During these multi-pod assemblages, individuals can share and subsequently learn certain behaviors (Whitehead, 2007). Over time, it is likely that more groups of killer whales will learn this behavior and begin targeting commercial fisheries where prey are easily located and available.

Documented injuries to killer whales range from minor to severe. Although some injuries appear to be life threatening, it is difficult to determine if an injury would lead to mortality of a whale. For example, the killer whale with the cut-off dorsal fin and severe head injury was seen feeding off discards. A killer whale in New Zealand that had its dorsal fin split into 2 parts reportedly lived for 2 years after the injury occurred (Visser and Fertl, 2000). It is unknown whether, but likely that, these severe injuries could be responsible for an early death. With all degrees and types of injuries, healing requires energy that could possibly lower a whale's resistance to disease. The underlying cause of a collapsed dorsal fin is unknown but could be attributable to either an injury or a whale's overall health, including nutritional issues.

Over half of the killer whales that were either killed by gear or killed by propellers and whose ecotype was

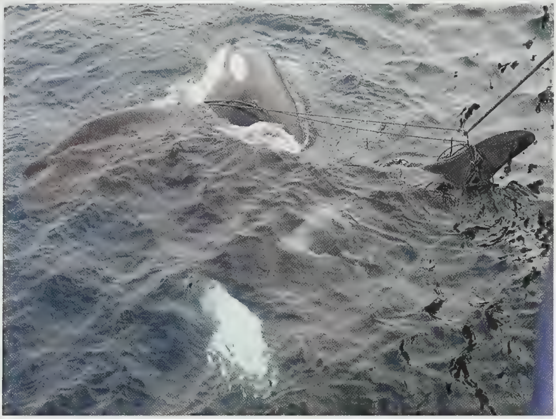

Figure 9

Photograph of a deceased adult male killer whale (*Orcinus orca*) entangled in longline gear (whale ID AK218; see Dahlheim, 1997) in the Bering Sea, taken during fishing operations in 2007.

determined through genetic analysis were of the resident ecotype. However, the 3 killer whales killed in net entanglements in the Alaska BSAI pollock trawl fishery, all juveniles, were found to be of the transient ecotype. Given that the diet of transient killer whales consists primarily of other marine mammals, we suggest that these whales were following pinnipeds (e.g., Steller sea lions, *Eumetopias jubatus*) that were in turn attracted to Alaska BSAI pollock trawling operations. The only photographs of transient killer whales collected by observers were taken when transient killer whales were killed and brought on board the vessel. Because transient whales are not targeting fish, their approaches may not be close enough to the boats to make it possible to take photographs usable for identification of ecotype.

It is unusual to find the large number of floating, dead killer whales encountered by observers because this species is thought to typically sink at death, preventing recovery. That a dead killer whale is found floating may indicate that the whale was recently killed (e.g., a whale entangled in gear and subsequently drowned) and then tossed back into the sea. Hence, mortalities could be as high as 43 individuals for this study period if the 16 killer whales found dead prior to fishery interactions are added to the 27 killer whales listed as killed as a result of interactions.

The Alaska groundfish fisheries operate in areas where killer whales are known to concentrate (Braham and Dahlheim, 1982). Major runs of salmon (*Oncorhynchus* spp.)

Table 2

Details about observations of killer whales (*Orcinus orca*) entangled in gear and subsequently released and their level of injury recorded between 2004 and 2013 in various Alaska Bering Sea and Aleutian Islands fisheries.

Year	Fishery	Comments	Level of injury determined
2004	Flatfish trawl	Caught in net, released by crew, and swam away. No injury noted, and no gear trailing.	Detailed data not available; therefore, level of injury listed as undetermined.
2012	Flatfish trawl	Caught in codend. Tried to unzip codend at least 2 times, but whale's fins caught in net. Finally cut whale free. Blood observed on deck, but unsure of level of injury. Whale swam away free of gear.	Serious injury concluded.
2012	Pacific cod longline	Tangled in longline gear. Crew attempted to untangle and cut off groundline. By the time crew got to the other end to view the animal, whale had untangled itself and swam off. No injury witnessed.	Whale not seriously injured.
2013	Flatfish trawl	Large orca caught in net. Took a bit of time to untangle. Whale appeared stunned or shocked, but once back in water it eventually swam back with other whales and was free of gear.	Serious injury concluded.
2013	Flatfish trawl	Small orca caught in net. Crew cut the net open on deck and pushed whale back in water. Whale swam off and back to the pod. No gear trailing.	Serious injury concluded.

Table 3

Details about tissues collected for genetic analysis from dead killer whales (*Orcinus orca*) brought aboard fishing vessels in various Alaska fisheries in the Bering Sea and Aleutian Islands (BSAI) and in the Gulf of Alaska (GOA) from 1999 through 2004. Genetic analysis was used to determine the ecotype of each whale: resident, transient, and offshore. Stock IDs were assigned by using ecotype and the region where the dead animal was sampled. All residents are identified as belonging to a single stock (i.e., the Alaska stock). Transient whales are identified as from either the AT1 stock or the GOA-BSAI stock. The age, sex, and cause of death recorded by observers for each whale are presented. A dash indicates that a whale's age class or sex was undetermined.

Sampling date	Fishery	Stock ID	Whale age class	Whale sex	Comment
20-Aug-1999	Pollock trawl	AT1 transient	Juvenile	F	Killed by gear
11-Aug-2001	Flatfish trawl	Alaska resident	Juvenile	–	Killed by propeller
12-Mar-2002	Pollock trawl	GOA-BSAI transient	Juvenile	–	Killed by gear
20-Mar-2003	Pollock trawl	GOA-BSAI transient	Juvenile	–	Killed by gear
22-Jul-2003	Pollock trawl	Alaska resident	Juvenile	M	Decomposed
9-Sep-2003	Pacifc cod longline	Alaska resident	Juvenile	F	Killed by gear
7-Apr-2004	Flatfish trawl	Alaska resident	Juvenile	M	Decomposed
21-Apr-2004	Flatfish trawl	Alaska resident	Juvenile	F	Hit by propeller
22-Apr-2004	Flatfish trawl	Alaska resident	–	F	Hit by propeller

and other fish species are seasonally available to killer whales in this area. It is no surprise that killer whales would be attracted to fishery operations knowing that food is easily available. Killer whales may not normally consume many of the fish species that they target during fishery interactions. Sablefish are found at depths ranging from 366 m to 1829 m (AFSC[9]), depths believed to be beyond the foraging capabilities of killer whales (Baird et al., 2005). Although an abundance of fish species are available for this ecotype, the availability and reliance on commercially caught fish and discards may likely cause populations of killer whales to increase. If the population level of killer whales is currently sustained by the dependence of whales on food obtained during commercial fishery operations, a significant reduction in the availability of caught fish coinciding with possible decreases in abundance of their natural prey (i.e., salmonids) may cause populations of killer whales to decline.

Conclusions

Our results provide information on the potential effects that commercial groundfish fisheries could have on Alaska killer whales, particularly the fish-eating resident stock. Given that 100% observer coverage is lacking for all fisheries and hauls, the total numbers of interactions, injuries, and mortalities reported here most likely represent underestimates. As currently defined, the Alaska resident killer whale stock ranges from Southeast Alaska to the Bering Sea (Muto et al., 2016). Results of recent studies indicate that the Alaska resident killer whale population may be more finely structured than previously thought, evidence of the likelihood of multiple stocks (Parsons et al., 2013). When compared to those of other cetaceans, populations of killer whales are small with low birth rates (Olesiuk et al., 1990; Dahlheim and Heyning, 1999); therefore, a take level that appears small may significantly affect a population of killer whales, especially if stock structure is found to be more finely structured. Within pods of resident killer whales, individual membership is stable over time and can consist of 2–3 generations. Given this social structure, the loss of a whale or whales from a pod may also have significant implications in how individuals in the pod respond to mortality events (Busson et al., 2019).

Given the long history of killer whales interacting with Alaska groundfish fishery operations (from the early 1960s to the present time) it is likely that interactions of killer whales with Alaska fisheries, events that lead to whale injuries and mortalities, will continue. The range where fishery interactions with killer whales occur may expand, and these interactions may become more frequent over time if the following scenarios occur: 1) the fishery expands in range and duration, 2) natural populations of fish stocks that are normally targeted by killer whales are reduced, 3) populations of killer whales increase, 4) more groups of killer whales learn this depredating behavior and start targeting fishing operations, and 5) killer whales become even more dependent on this reliable food source.

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[9] AFSC (Alaska Fisheries Science Center). 2021. Alaska sablefish fisheries and assessment. Website. [Last modified 27 August 2021.]

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Preparation of manuscript

Title page should include authors' full names, affiliations, mailing addresses, and the senior author's email address.

Abstract should be limited to 200 words (one-half typed page), state the main scope of the research, and emphasize the authors' conclusions and relevant findings. Do not review the methods of the study or list the contents of the paper. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely.

General text must be typed in 12-point Times New Roman font throughout. A brief introduction should convey the broad significance of the paper; the remainder of the paper should be divided into the following sections: Materials and methods, Results, Discussion, Conclusions, and Acknowledgments. Headings within each section must be short, reflect a logical sequence, and follow the rules of subdivision (i.e., there can be no subdivision without at least 2 subheadings). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be written out in full and defined the first time they are mentioned. Abbreviations should be used sparingly because they are not carried over to indexing databases and slow readability for those readers outside a discipline. They should never be used for the main subject (e.g., species or method) of a paper.

For general style, follow the U.S. Government Publishing Office *Style Manual* (2016, available at website) and *Scientific Style and Format: the CSE Manual for Authors, Editors, and Publishers* (2014, 8th ed.) published by the Council of Science Editors. For scientific nomenclature, use the current edition of the American Fisheries Society's (AFS) *Common and Scientific Names of Fishes from the United States, Canada, and Mexico* and its companion volumes (*Crustaceans, Mollusks, Cnidaria and Ctenophora*, and *World Fishes Important to North Americans*). For species not found in the previously mentioned AFS publications and for more recent changes in nomenclature, use the Integrated Taxonomic Information System (ITIS, available at website), or, secondarily, the California Academy of Sciences *Catalog of Fishes* (available at website) for species names not included in ITIS. Common (vernacular) names of species should be lowercase. Citations must be given for the identification of specimens. For example, "Fish species were identified according to Collette and Klein-MacPhee (2002); sponges were identified according to Stone et al. (2011)."

Dates should be written as follows: 11 November 2018. Measurements should be expressed in metric units, for example, "58 metric tons (t);" if other units of measurement are used, please make this fact explicit to the reader. Use numerals, not words, to express whole and decimal numbers in the general text, tables, and figure captions (except at the beginning of a sentence). For example, "We considered 3 hypotheses. We collected 7 samples in this location." Use American spelling. Refrain from using the shorthand slash (/), an ambiguous symbol, in the general text.

Cite all software, special equipment, and chemical solutions used in the study within parentheses in the general text, including the version number, company name, and the city and state (or nation) of the company headquarters, for example, "SAS, vers. 9.4 (SAS Institute Inc., Cary, NC)."

Word usage and grammar that may be useful are the following:

- *Aging*

  For our journal, the word *aging* is used to mean both age determination and the aging process (senescence). Authors should make clear which meaning is intended where ambiguity may arise.

- *Fish and fishes*

  The plural of the word fish (a collective noun that implies individuals without regard to species) is *fish*.

  Example: The *fish* were collected by trawl net.

  Example: The numbers of *fish* collected that season were less than the numbers from previous years.

  The plural for *fish species* is *fishes* (a contrived plural used by taxonomists to mean several or more *fish species*) or one can use *fish species* (which is preferred in this journal for clarity across disciplines).

  Example: The *fishes* of Puget Sound [biodiversity is implied] or

  Example: The *fish species* of Puget Sound [preferred plural for clarity across disciplines].

- *Crab and crabs, squid and squids, etc.*

  The plural of the word *crab* (i.e., many individuals without regard to species) is *crab*.

  Example: The crab were sorted by weight.

  Example: Many red king *crab* were dying [Many individuals of one species of crab.]

  The plural of *crab species* is *crabs* (a word used by taxonomists) or *crab species* (the latter is preferred in this journal for clarity).

  Example: These *crabs* were selected for treatment. [Different crab species are implied.]

  Example: These *crab species* were selected for treatment. [Preferred word choice for clarity.]

  Example: Snow *crabs* are found throughout the North Pacific Ocean and Bering Sea. [There are 2 species of snow crab; therefore the word *crabs* can be used here.]

  Example: *Two species* of snow *crab* are found throughout the North Pacific Ocean and Bering Sea. [Preferred usage for clarity.]

  Example: Three crabs were selected for treatment. [3 species of crab are implied.]

  Example: Three crab species were selected for treatment. [Preferred word choice for clarity.]

- We use *fisherman* and *fishermen*, not *fisher* and *fishers*, in this journal. One can always use crew member, vessel operator, and angler (the latter for recreational fishing).

- *The definite article with common names of species*

  When the singular common name of a species represents the entire class or group to which it belongs, use the definite article.

  Example: Only one species of the genus *Salmo* is found in the Atlantic Ocean—*the* Atlantic salmon (*Salmo salar*).

  Example: The sonic emissions of *the* bottlenose dolphin are complex.

  For plural common names, this rule does not apply.

  Example: Chinook salmon are found throughout the Pacific Ocean.

  Example: Bottlenose dolphins are found in temperate and tropical waters.

- *Sex*

  For the meaning of male and female, use the word *sex*, not *gender*. Do not write, "fish were sexed." Write, "sex was determined."

- *Participles*

  As adjectives, participles must modify a specific noun or pronoun.

  Example: Using mark-recapture methods, these scientists determined the size of the population. [Correct. The participle *using* modifies the word *scientists*.]

Example: These scientists, based on the collected data, concluded that the mortality rate of these fish had increased. [Incorrect. The scientists were not based on the collected data.]

Example: These scientists concluded, on the basis of collected data, that the mortality rate of these fish had increased. [Correct. The offending participle has been eliminated and an adverbial phrase modifies the verb *concluded*.]

Equations and mathematical symbols should be set from a standard mathematical program (MathType or Equation Editor). Equations formatted in LaTex are not acceptable. For mathematical symbols in the general text (α, χ^2, π, ±, etc.), use the symbols provided by the MS Word program and italicize all variables, except those variables represented by Greek letters and the superscript and subscript parts of variables and expressions. Do not use photo mode when creating these symbols in the general text, and do not cut and paste equations, letters, or symbols from a different software program.

Number equations (if there are more than one) for future reference by scientists; place the number within parentheses at the end of the first line of the equation.

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Acknowledgments should be no more than 6 lines of text. Only those who have contributed in an outstanding way should be acknowledged by name. For recognition of other persons or groups, use a general term, such as *crew*, *observers*, or *research coordinators*, and do not include names with these terms.

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Tables are often overused in scientific papers; it is seldom necessary to present all the data associated with a study. Tables should not be excessive in size and must be cited in numerical order in the text. Headings should be short but ample enough to allow the table to be intelligible on its own.

All abbreviations and unusual symbols must be explained in the table legend. Other incidental comments may be footnoted with numeral footnote markers. Use asterisks only to indicate significance in statistical data. Do not put a table legend on a page separate from the table; place the legend above the table. *Do not submit tables in photo mode.*

- Note probability with a capital, italic P.
- Provide a zero before all decimal points for values less than one (e.g., 0.07).
- Round all values to 2 decimal points.
- Use a comma in numbers of 5 digits or more (e.g., 13,000 but 3000).

Figures must be cited in numerical order in the text. Graphics should aid in the comprehension of the text, but they should be limited to presenting patterns rather than raw data. The number of figures should not exceed 1 figure for every 4 pages of text.

Figure legends should explain all symbols and abbreviations seen in the figure and should be double spaced on a separate page at the end of the manuscript.

Line art and halftone figures should be saved at resolutions >600 dots per inch (dpi) and >300 dpi, respectively. Color is allowed in figures to show morphological differences among species (for species identification), to show stain reactions, to show gradations (such as those of temperature and salinity within maps), and to distinguish between numerous lines and symbols in graphs. Figures approved for color should be saved in CMYK format.

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- Capitalize only the first letter of the first word and proper nouns in all labels within figures.
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- Do not include vertical and horizontal lines in the background of graphs. Ticks for values on the x-axis and y-axis will suffice.
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Supplementary materials that are considered essential, but are too large or impractical for inclusion in a paper (e.g., metadata, figures, tables, videos, and websites), may be provided at the end of an article. These materials are subject to the editorial standards of the journal. A URL to the supplementary material and a brief explanation for including such material should be sent at the time of initial submission of the paper to the journal.

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